THE TALITROIDEAN AMPHIPOD FAMILY HYALIDAE REVISED, WITH EMPHASIS ON THE NORTH PACIFIC FAUNA: SYSTEMATICS AND DISTRIBUTIONAL ECOLOGY.

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ABSTRACT

Analysis of hyalid species of coastal waters of the North Pacific Basin based on newly recognized characters (e.g., hydrodynamic lobes of the gnathopods, surge seta and notch of the posterior margin of the bases of peraeopods 5-7), and those recently utilized elsewhere (e.g., pre-amplexing notch of peracon 2 female, posterior marginal cusps of coxae 1-4, and form of brood lamellae and marginal setae), necessitated establishment of new generic concepts and family reconstitution on a world-wide basis. Hyalidae here encompasses subfamilies Hyalinae Rathke (new status) based on *Hyale* Rathke sens. str.; Kuriinae J. L. Barnard (new status), based on *Kuria longimana* Scott & Walker and *Micropythia* Krapp-Schickel; and **Hyacheliinae** new subfamily, based on *Hyachelia tortugae* J. L. Barnard. Subfamily Hyalinae encompasses two morphological-behavioural groups of genera: (1) a relatively primitive natator group, hydrodynamically specialized for swimming, that includes *Parallorchestes* Shoemaker, ***Protohyale*** n. g., *Lelehua* J. L. Barnard, *Hyale* Rathke sens. str., and the enigmatic genus *Neobule* Haswell (***Protohyale*** encompasses ***Boreohyale*** n. subg., ***Diplohyale*** n. subg., ***Leptohyale*** n. subg., and *Protohyale*, nominate subgenus; and (2) a relatively advanced mainly intertidal saltator group (specialized for jumping or springing in air) that encompasses *Parhyale* Stebbing, ***Ptilohyale*** n. g., ***Apohyale*** n. g., ***Ruffohyale*** n. g., and ***Serejohyale*** n. g. Newly described from the Pacific coast of North America are: ***Parallorchestes alaskensis*** n. sp., ***P. carinata*** n. sp., ***P. cowani*** n. sp., ***P. kabatai*** n. sp., ***P. leblondi*** n. sp., ***P. minima*** n. sp., ***P. nuda*** n. sp., ***P. subcarinata*** n. sp., and ***P. trispinosa*** n. sp. Also redescribed are *P. americana* Bousfield, and three western N. Pacific species: *P. asiatica* Tzvetkova, *P. ochotensis* (Brandt) and *P. zibellina* (Derzhavin). *Protohyale* encompasses within subgenus ***Boreohyale*** the following N. American Pacific species: ***P. (B.) hiwatarii*** n. sp., ***P. (B.) jarrettae*** n. sp.,***P. (B.) lamberti*** n. sp., ***P. (B.) neorionensis*** n. sp., ***P. (B.) oclairi*** n. sp., ***P. (B.) oculata*** n. sp., ***P. (B.) seticornis*** n. sp., and within the monotypic subgenus ***Leptohyale, P. (L.) longipalpa,*** n. sp. Species within subgenus *Protohyale* occur in southern California and Baja California (Mexico), including *P. (P.) canalina* (Barnard), *P. (P. frequens* (Stout), ***P. (P.) mohri*** n. sp., and *P. (P.) yaqui* (Barnard). North American Pacific saltating hyalids include ***Apohyale*** *anceps* (Barnard), ***A.*** *californica* (Barnard), ***A.*** *pugettensis* (Dana) and ***Ptilohyale*** *plumulosa* (Stimpson). Keys, illustrations, and numerical taxonomical and distributional analyses are also provided. The cold-temperate hyalids of eastern and western North Pacific hyalids are not closely related, and the warm-temperate hyalids of the western Pacific have closer affinities with those of the central Pacific (Hawaiian) archipelago.

INTRODUCTION

Species of Hyalidae occur mainly intertidally and in shallow littoral marine waters. Although not usually conspicuous because of their relatively small size and somewhat concealed life style, these aquatic talitroideans were nonetheless among the earliest amphipod species recorded and described from the coasts of Eurasia (e.g., Rathke 1837; Kroyer 1845; Bate 1856) and newly colonized Pacific continental coasts during the 19th century (e.g., Dana 1853; Stimpson 1857). Nineteenth century records were summarized by Stebbing (1906) and early 20th century records by Holmes (1904), Stout (1913), and Thorsteinson (1941).

The authors are enormously indebted to the late J. L. (Jerry) Barnard whose publications on the littoral marine amphipods of California, Baja, Hawaii, and Galapagos regions (1970, 1974,1979), and earlier studies (1952, 1954, 1955, 1962, 1965, 1969b, 1975) laid a solid foundation for the present investigation. Popularized compendia including those of Ricketts and Calvin (1948), Smith & Carlton (1975), Austin, (1985) and Staude (1987) provide regional lists and keys to species of the northwestern Pacific coast.

Essential elements of the present study of the North Pacific hyalids were first summarized by Bousfield (1981). As this summary was to be accompanied by full taxonomic treatment of new taxa elsewhere, the illustrations were small, unaccompanied by formal diagnoses, or identification of type specimens and type localities. Regrettably, the intended publication series (Bulletin of the National Museum of Natural Sciences, Canada) was discontinued shortly thereafter. The intended treatise (Bousfield MS), bearing essentially the same title as the present, did not appear, thus rendering the present paper in effect an "interrupted publication" (ICZN 1985, article 23). Consequently, the names (1981) that were apparently considered unavailable *(nomina nuda)* by most subsequent authors, including

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definitive gammaridean amphipod treatments (e.g., Barnard & Karaman 1991; Ishimaru 1994) are herein validated by formal description (ICZN). The present study is intended, therefore, to complete formal description of these new taxa under new names, and expand the work into a preliminary world-wide review of the entire family Hyalidae.

Taxonomic knowledge of the family has increased rapidly elsewhere. Thus, during the past 35 years the family has increased from 60 described species (Barnard 1969a) to the present ~110 species in 12 genera and three subfamilies.

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For assistance with field work the authors are greatly indebted to regional marine laboratories, notably the Pacific Biological Station, Nanaimo, B. C., the Pacific Environmental Institute, West Vancouver, B. C., the Bamfield Marine Station, B. C., and the Friday Harbor Laboratories, WA. Much of the detail has been acknowledged in previous station lists (below). Drs. Craig P. Staude and Colin B. Levings, and the late Drs. Josephine F. L. Hart, and Daniel B. Quayle were especially helpful with the field work.

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Taxonomic work on CMN amphipod collections was performed initially by ELB as a staff member of the National Museum of Natural Sciences at the Holly Lane Laboratory, Ottawa, during the period 1979-1985, and more recently as a visiting scientist. Original line illustrations were prepared with the capable assistance of artist Floy E. Zittin, Cupertino, California. The authors are indebted to Marjorie Bousfield for translations of the Russian literature.

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Table I. Abbreviations used in figures and tables:

A1-2	-	antenna 1, 2
BAS	-	basis
BR SET	-	brood seta(e)
CARP	-	carpus
CLSP	-	clothes-pin spine
CX	-	coxal plate
DCTL	-	dactyl
EP 1-3	-	abdomin. side plates 1,.2,3
GN 1-2	-	gnathopods 1, 2
HD	-	head
ISCH	-	ischium
LFT	-	left
LL	-	lower lip (labium)
MD	-	mandible
MER	-	merus
MX 1-2	-	maxilla 1, 2
MXPD	-	maxilliped
P3-7	-	peraeopods 3, 4, 5, 6, 7
P-AMP NTCH	-	preamplexing notch
PLPD	-	pleopod
PLP	-	palp
PRPD	-	propod
RET	-	retinacula
RT	-	right
SG SET	-	surge seta
SP	-	spine
T	-	telson
U1-3	-	uropod 1, 2, 3
UL	-	upper lip (labrum)
UROS	-	urosome
X	-	enlarged
im	-	immature
juv	-	juvenile
subad.	-	subadult

MATERIALS AND METHODS.

Station lists pertinent to field material utilized in this study are provided in Bousfield (1958, 1963, 1968); Bousfield & McAllister (1962); and Bousfield & Jarrett (1981). Numbers of specimens collected at each station are given in parentheses.

Analyses of possible phyletic relationships of hyalid genera and species utilize a semi-phyletic modification of the UPGMA system of Sneath and Sokal (1973). Characters and character states are illustrated mainly in Figures 1-4. These are ordered phyletically by values of 0, 1, and 2 for plesiomorphic, intermediate, and apomorphic states, respectively. The phyletic placement of a given taxon is represented by a numerical sum of character state values termed the Plesio-Apomorphic (P.-A.) Index of which the maximum value is twice the number of characters utilized.

SYSTEMATICS

HYALIDAE Bulycheva

Hyalidae Bulycheva, 1957: 76;—Bousfield 1982: 269;—Bousfield 2001a: 104;—Serejo 2001: 480.
Hyalidae (part): Barnard & Karaman 1991: 366;—Bousfield & Shih 1994: 129;—Ishimaru 1994: 67;—Lowry & Springthorpe 2002.
Hyalinae (Talitridae) (part) Barnard 1972:167;—Griffiths 1976: 76.
Talitridae (part) Stebbing 1906: 523;—Gurjanova 1951: 813.
Talitroidea (part) Barnard 1969a: 463;—Barnard & Barnard 1983: 161.

Subfamilies: Hyalinae Rathke,1837, restricted status; **Hyacheliinae** n. subfam.; Kuriinae Barnard, 1964, new status.

Diagnosis: Body smooth or posteriorly middorsally toothed. Antennae well developed; Antenna 1 longer than peduncle of antenna 2; gland cone small.

Mandible, left lacinia 5-8 dentate. Maxilla 1, palp slender,1-2 segmented. Maxilla 2, inner plate with 1 (2) plumose inner marginal seta(e). Maxilliped, plates well developed, palp large, occasionally sexually dimorphic (dactyl often with apical whip flagellum in male).

Coxal plates 1-4 normal, medium deep; posterior marginal shelf and cusp variously developed, reduced, or lacking. Coxae 5 slightly anterolobate. Coxal gills medium to large, plate-like or sac-like.

Gnathopod 1 small, regularly subchelate, propod and/or dactyl variously sexually dimorphic; basis often with anterodistal hydrodynamic lobe; dactyl simple, occasionally bidentate or bifid (male). Gnathopod 2 usually strongly sexually dimorphic; basis & ischium often with hydrodynamic lobes; carpal lobe developed (female) or mostly lacking (male); propod and dactyl strongly developed (male).

Peraeopods 3-7 regularly ambulatory,"perching" or prehensile (Hyacheliinae). Peraeopods 5-7 essentially homopodous; bases broad, hind margin variously crenulated, usually with submedian notch and "surge seta"; propod often with anterior marginal clasping spine(s); dactyl strong and simple, or relatively short, with strong inner marginal seta.

Epimeral plates regular, weakly armed. Pleopod rami normally developed, natatory. Uropod 1, peduncle and rami subequal in length; peduncle often with strong distal spine(s); rami linear, marginally spinose. Uropod 2 similar, smaller, outer ramus often shorter. Uropod 3 short, spinose, essentially uniramous, or with inner ramus reduced to a small lobe.

Telson short, fully bilobate, lobes subtriangular.

Mature Female: Gnathopods regularly subchelate, subsimilar. Brood lamellae variously subovate, sublunate, or subrhomboidal in outline, margins lined with numeorus hook-tipped setae. Peraeon segment 2 antero-distal margin usually with pre-amplexing notch.

Habitat: Marine littoral, free-swimming or intertidal and saltatory, often associated with algae and marine grasses; nearly cosmopolitan (except polar regions), along temperate to tropical, mainly rocky, surf-exposed, high-salinity shores; a few species are estuarine and brackish-water, and members of one genus are hypogean in coastal freshwaters.

Remarks: Implementation of names of taxa, newly utilized in previous publications but taxonomically unavailable, here conform with rulings set forth in the ICZN Code (1985 and 1999), Sect. 18, Art. 23. Apparently for the reason of taxonomic unavailability, Barnard & Karaman (1991) and Ishimaru (1994) did not include new species names proposed by Bousfield (1981) for North American Pacific species of *Hyale* Rathke sens. lat. and *Parallorchestes* Shoemaker. Although most of these species were again listed, and four new generic names added by Bousfield (2001a), all but one name remained technically as *nomina nuda*. The exception was *Parallorchestes americana* Bousfield, 1981, recognized and validated through detailed comparison of

its character states with those of the western Pacific species, *P. asiatica* Tzvetkova, 1990. In following the provisions of ICZN rulings (above), the authors have here fully described and figured, and hence taxonomically validated, many of the original names; in some instances, however, alternate new names have been proposed, as detailed in the following descriptive accounts of hyalid subfamilies, genera and species.

Almost uniquely among malacostracan crustaceans, the basic amphipod body form is designed for sustained rapid forward swimming (Boudrias 1991). Mysidaceans also propel themselves forward, but since the body and appendages are streamlined, the forward motion is short, jerky, and unsustained (personal observations on specimens of *Praunus flexuosus in aquaria*). Although synchroflash, cinephotographic evidence is not yet available, a primary function of the subsimilar, large-plated peraeopods, overlapping forwards and backwards from the "shoulder" or "beam" segment (peraeon 5), would appear to be streamlining of the lateral body surfaces during swimming. The large rounded basal plates of peraeopods 5-7 may also serve in rudder-like steering and/or "braking" action by means of an alternate, or simultaneous, controlled outward extension of their trailing edges. The lobes of the bilobate telson may also serve in steering and/or elevation during swimming. Such presumably adapts members of family Hyalidae for swimming and benthic "perching" (of Steele 1988) in the strongly lotic conditions of surf-exposed coastal marine littoral and sublittoral habitats.

By contrast, described members of closely related family Hyalellidae Bulycheva (see Hendrycks & Bousfield 2001) are ambulatory, algal-dwelling, and semi-fossorial, mainly in temperate and tropical marine and freshwater sedimentary bottoms. In all hyalellid species, the basal and ischial segments of gnathopods 1 & 2 (both sexes) totally lack anterodistal hydrodynamic lobes; the basal segments of peraeopods 5-7 lack posterior marginal notch and "surge seta"; the distolateral and distomedial peduncular spines of uropod 1 are not enlarged; and the telson lobes have become basally fused (e.g., in *Allorchestes*) or totally fused as a solid plate (e.g., in *Hyalella, Parhyalella*), and of possibly different primary function. Freshwater members of family Hyalellidae possess sternal gills, and often processiferous body segments, but less robust peraeopods and uropods.

The website version of Hyalidae by Lowry (1999), and Lowry and Springthorpe (2001) follows that proposed by Barnard & Karaman (1991). The version was apparently not subject to numerical analysis of character states then considered significant. More recently, alphabetical compendia have increasingly been superseded by phyletically oriented generic- and family-level revisions in which new and important character states have been recognized and the results supported by numerical analysis. Since 1986, these studies, including the present, have increased the world total by ~20% more species and ~30% more genera. We hope therefore, that the present comprehensive analysis of family Hyalidae will more concisely define its diagnostic character states and generic inclusions, and underline its morphological, distributional-ecological, and behavioural differences from other families within superfamily Talitroidea.

Subfamily Hyalinae restricted status

Hyalinae (part) Barnard 1972:167;—Griffiths 1976: 76.

Type genus: *Hyale* Rathke, 1837.

Genera: ***Apohyale*** n. g. (p. 104); *Hyale* Rathke, 1837 (p. 9); *Lelehua* Barnard, 1970 (p. 92); *Neobule* Haswell, 1880 (not treated); *Parallorchestes* Shoemaker, 1941 (p. 36); *Parhyale* Stebbing 1899 (p. 96); ***Protohyale*** n. g. (p. 62) [***Boreohyale*** n. subg.; ***Diplohyale*** n. subg., ***Leptotohyale*** n. subg.; ***Protohyale*** nom. subg.]; ***Ptilohyale*** n. g. (p. 98); ***Ruffohyale*** n. g. (p. 116); ***Serejohyale*** n. g. (p. 114).

Diagnosis: Small to medium large, free-living, morphologically and behaviourally basic members of the Talitroidean Reptantia. Combinational diagnostic character states include: Antenna 2 medium to elongate.

Coxal plates 1-4, posterior marginal "shelf and/or cusp often strongly developed. Coxal gills large,plate-like or sac-like. Sternal gills lacking.

Gnathopods 1 & 2 subchelate, strongly differing in form and size (male), subsimilar (female); gnathopod 1 weakly, and gnathopod 2 usually strongly sexually dimorphic. Hydrodynamic lobes of basis and ischium of gnathopods variously developed (both sexes).

Peraeopods 5-7; basis broad, hind margin often crenulated, with single notch and "surge seta".

Pleopods slender, with reduced retinacula, but fully developed plumose-setose rami. Uropods 1 & 2, rami stout, marginally irregularly spinose (not slender, serially spinose and natatory). Uropod 3 uniramous or

weakly biramous. Telson short, fully bilobate. Brood lamellae large, broad,variously subovate to subrhomboidal. Preamplexing notch present.

Remarks: Subfamily Hyalinae encompasses all but three described species of family Hyalidae, assigned to subfamilies Kuriinae and the Hyacheliinae. Within Hyalinae, the stout strongly spinose distal segments of the peraeopods would appear specially adapted to grasping or perching upon algae and other bottom substrata located in strongly lotic waters such as the surf zone of rocky beaches of tropical and temperate marine regions.

Barnard (1972) and Griffiths (1974, 1976) departed from the original talitroidean classificatory concepts of Bulycheva (1957) in relegating members of families Hyalidae and Hyalellidae to subfamily status (as Hyalinae) within family Talitridae. However, evidence revealed by the present study provides greater support for continued recognition of the orginal concepts of Bulycheva (loc. cit.).

Characters and Character states

The main characters and their possible states within the Hyalinae (Figs. 1-3) require little clarification here, unlike the five characters discussed below.

1. Hydrodynamic (h.-d.) lobes of the gnathopods.

The design of the body and appendages of amphipod crustaceans is unique within malacostracan crustaceans in maximizing sustained forward swimming speed. Hydrodynamic efficiency is facilitated through a forward-thrusting abdominal propulsion unit (3 pairs of pleopods and tail-fan of 3 pairs of uropods and telson), and the streamlined form and position of body plates and appendages. Such includes, in all amphipod custaceans, the forward-overlapping of coxal plates 1-4, forward of "beam" peraeon segment 5 (widest body segment), and the backwards overlapping of basal, coxal, and epimeral plates posteriorly from that segment. Coxa 5 (at the "beam"),universally within the Amphipoda, overlaps neighbouring plates both forwards and backwards. In addition, body spines and carinations of swimming amphipods are located mainly behind peraeon segment 5 and point posteriorly.

By contrast, within caridean and most decapod shrimps (e.g., *Homarus americanus*), the "beam" is at abdominal segment 2. The epimeral plate of that segment overlaps adjacent plates forward and backards and facilitates rapid backwards propulsion ("escape reaction") by the tail fan. Body and rostral spines of swimming decapods are located mainly on the cephalothorax and point anteriorly.

A review of limited information and theoretical considerations concerning the hydrodynamics of gammaridean amphipods, especially of members of superfamily Lysianassoidea, is provided by Boudrias (1991). Supplemental information on streamlining of body and appendages in hyperiid amphipods (e.g., within superfamily Platysceloidea) is provided by Bowman and Gruner (1973), and on swimming speeds by Takeuchi & Watanabe (1998), Sainte-Marie (1986), and theoretical consideration herein.

Broadly across genera of subfamily Hyalinae, the basis and ischium of gnathopods 1 & 2 are variously modified into large rounded lobes on the anterodistal segmental margins (nasiform lobe of Barnard 1979). These overlap on the adjacent segments hydrodynamically forwards (Fig. 4). Their margins are rounded, presumably to facilitate flexing of the segments and maintain streamlined form at normal angles of flexure. The lobe of the basis is positionally anterodistolateral whereas the lobe of the ischium is mainly anterolateral.

The purpose of the lobe has not yet been tested experimentally. However, morphological and behavioural evidence indicates to us that its principal function is to streamline margins of appendages that are folded during swimming (see also Figs. 5-7). The appellation "hydrodynamic" or "h.-d."lobe is used henceforth in this study.

The distribution and strength of development of the hydrodynamic lobe on the basal and ischial segments of gnathopods 1 & 2 is outlined graphically in fig. 4. Lobes are most strongly developed within the natatory genus *Protohyale*, and intermediate or least strong in members of saltatory genera such as *Ptilohyale, Apohyale* and *Parhyale*. Lobes are generally less well developed in the smaller gnathopods of females than in the larger gnathopods of males. Thus, even within *Protohyale*, the ischial lobe is not well developed in gnathopod 2 of the female. Ischial lobes are weakly developed in males of *Parhyale* and *Ptilohyale*, and apparently lacking in females of *Lelehua* and *Hyale*.

Leite and Wakabara (1989) studied developmental changes in the form and armature of gnathopod 2 of males and females of *Protohyale (P.) media* (Dana). Although these authors beautifully illustrated carpus, propod and dactyl, they did not treat the significance of corresponding changes in the anterodistal (hydrodynamic) lobes of the basis and ischium. For this purpose, pertinent parts of their figures are reproduced here (Figs. 5 & 6). In the male (Fig. 5), the h.-d. lobe of

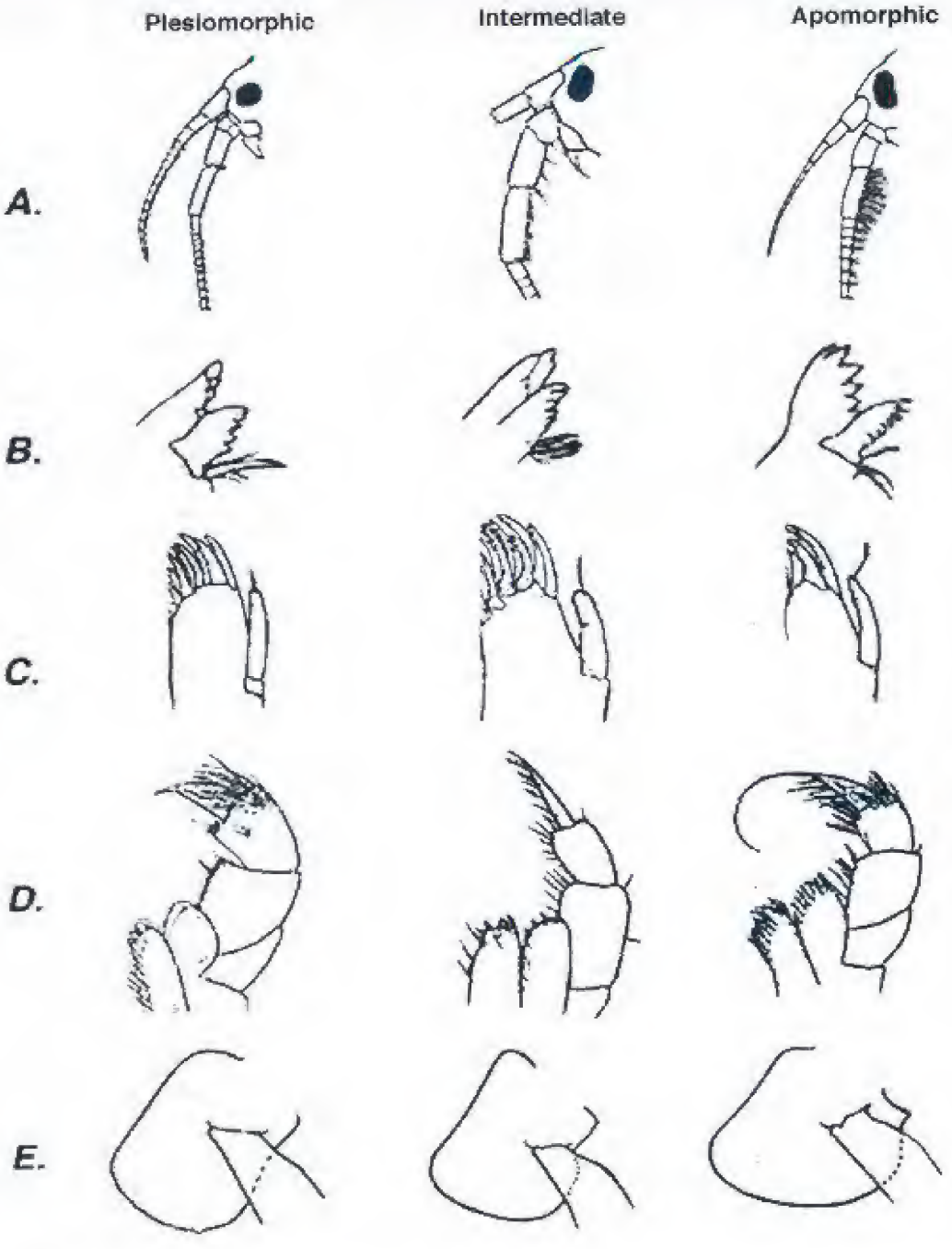

Fig. 1. Characters and Character States of Hyalinae. A. Eye shape and antenna 2: setation; B. Mandibular left lacinia: dentation C. Maxilla 1: segmentation of palp; D. Maxilliped palp: form of dactyl (♂). E. Coxa 1, posterior marginal shelf & cusp.

basis and ischium are in early development stages during the 6th to 4th last instars. They attain fully lobate and overlapping form in the final three instars, coincident with complete fusion of the unguis to the body of the dactyl, and presumably full sexual maturity. In the female (fig. 6), the h.-d. lobe of the basis follows a similar progression,and attains fully lobeate conditon in the final two instars. That of the ischium attains only very small size by the final instar. Such evidence might suggest that presence of large hydrodynamic lobes of the gnathopods is an advanced character state in hyalid amphipods. As their development to small size only in intertidal saltating species might result fromneotenic loss, the phyletic significance of this character state remains moot. Corresponding studies on developmental stages of gnathopod 1 (male), and the preamplexing notch of peraeon 2 (female) may prove instructive in clarifying this point.

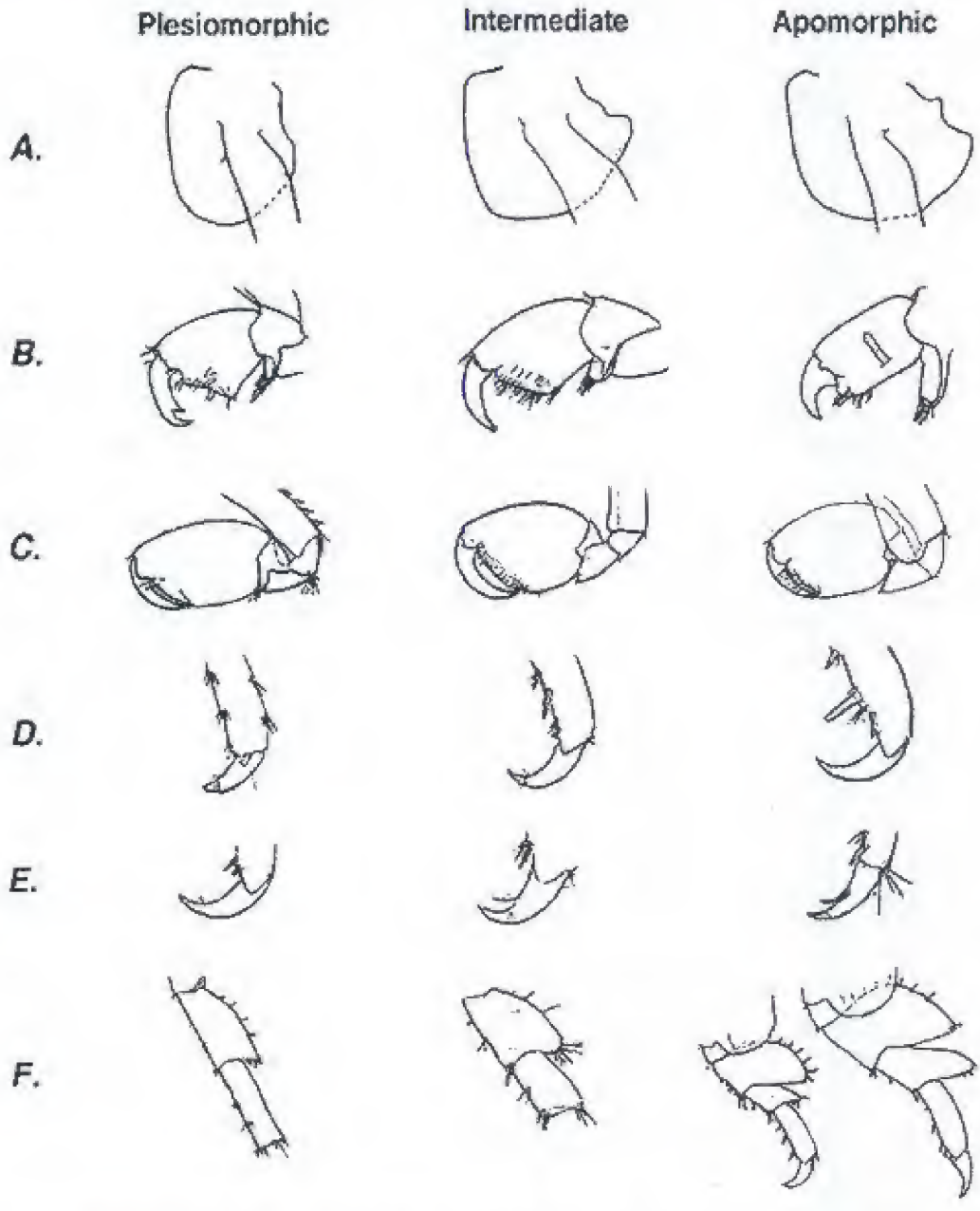

Fig. 2. Characters and Character States of Hyalinae. A. Coxa 4: posteror marginal cusp; B. Gnathopod 1 (♂); preamplexing spines of propod; C. Gnathopod 2 (♂): size of carpal lobe; D. Peraeopods 5-6; size of clasping spine; E. Dactyl of peraeopods 5-7: size of inner marginal seta; F. Peraeopods 5-7: degree of broadening of segment 4 (Literature sources).

The presence of hydrodynamic lobes in the Hyalinae (and Hyachelinae) is here considered a secondary but plesiomorphic character state. Its strong expression in mainly free-swimming genera of Hyalinae (Fig. 4) especially in warm-temperate and tropical groups such as *Protohyale*, tends to support the present concept of hydrodynamic functionality. Thus, streamlining of gnathopods in the swimming or "tuck" position presumably facilitates a rapid escape reaction from fast-swimming predators or quick movement from lotic surf waters or tidal currents into suitable benthic niches for food and shelter.

Elsewhere within theTalitroidea, well-developed hydrodynamic lobes have been detected on the basal and ischial segments of gnathopod 2 of mature males of most palustral genera of family Talitridae [see fig.7 , and Bousfield 1973, 1984]. In these species that are submerged for part or most of a tidal cycle (e.g., in *Eorchestia, Protorchestia, Uhlorhestia*) or that occur in freshwater (e.g., *Chiltonorchestia)*, the lobes occur

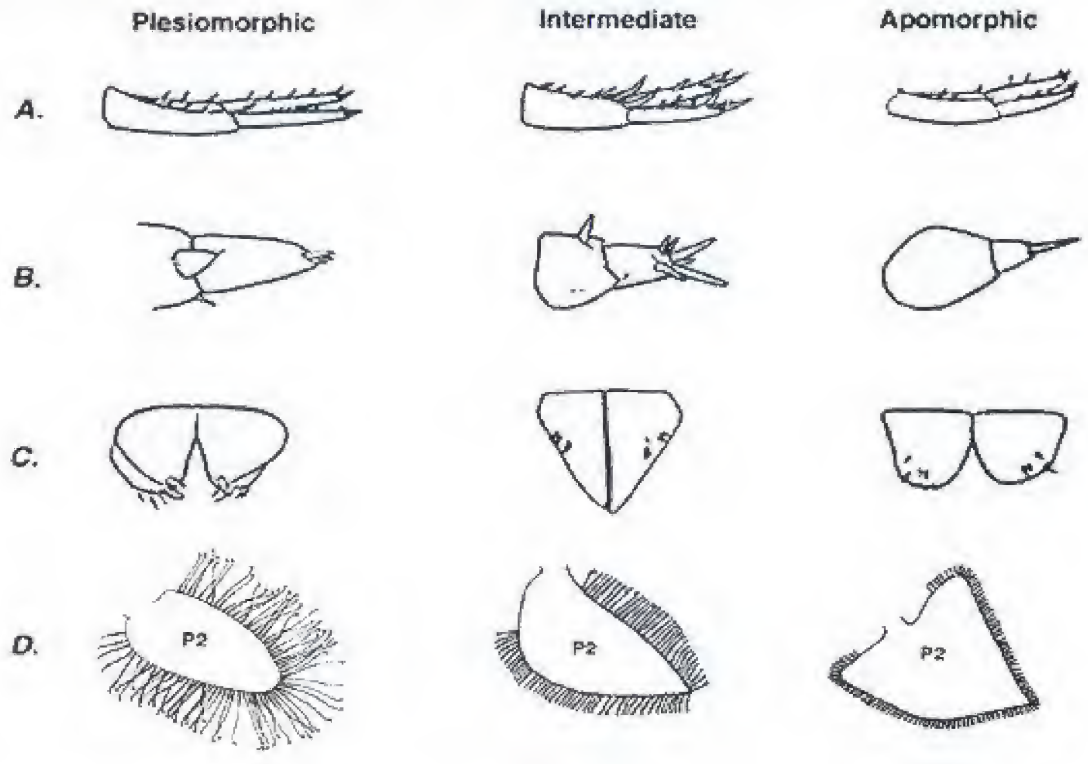

Fig. 3. Characters and character states of Hyalinae.
A. Uropod 1, peduncular distal spine(s); B. Uropod 3, number of rami;
C. Telson, form and armature; D. Brood plate (peraeopod 2, ♀), form and marginal setation.

anterodistolaterally on the basis, and both antero-laterally and anteromedially on the ischial segment (fig. 7). The lobes are generally less strongly developed in beachflea genera (e.g., *Orchestia, Tethorchestia, Platorchestia*, and a few primitive terrestrial genera (e.g., *Cerrorchestia spp., Orchestiella neambulans*) (see Lindeman 1991; Friend 1987). They are weakly developed or lacking in sandhopper genera (e.g., *Americorchestia, Megalorchestia, Sinorchestia)* (see Bousfield 1982, 1992; Morino 1972). Hydrodynamic lobes are weakly developed on the basis and ischium of males within subfamily Chiltoniinae (Hyalellidae), but apparently not developed (secondarily lost?) in other families and subfamilies of Talitroidea.

Hydrodynamic lobes of gnathopods are known elsewhere within gammaridean amphipods, but an exhaustive review of their occurrence is beyond the scope of this study. A few samples may illustrate the phenomenon. Thus, within the advanced tube-building superfamily Corophioidea, well developed lobes of similar type have been illustrated in the powerfully subchelate gnathopod 2 of males of family Ampithoidae (e.g., *Ampithoe valida, Peramphithoe plea*), family Ischyroceridae (*Ischyrocerus oahu, Parajassa angularis*), and in some Isaeidae (e.g., *Photis kapapa*), and in gnathopod 1 of family Aoridae (e.g., *Aoroides*) but not in family Dulichiidae [see Bousfield, 1973; Barnard 1970a; Barnard & Karaman, 1991]. Within more primitive benthic superfamilies (e.g., Leucothoidea), paired ischial lobes are present in the powerfully subchelate gnathopods 1 & 2 of both sexes within family Pleustidae (e.g., *Pleustes tuberculatus, Thorlaksonius borealis*) [see Bousfield & Hendrycks 1994], family Amphilochidae (e.g., *Apolochus litoralis, Hourstonius vilordes*), and in males within superfamily Stenothoidea (e.g., *Stenothoe marina, Metopella angusta*). The anterior basal lobes of gnathopod 2 within the Cyamida (e.g., *Cyamus, Scutocyamus*) may be considered hydrodynamic lobes, even though the animal itself remains stationary (Margolis et al 2000). The lobes presumably facilitate smooth laminar flow of strong water currents resulting from rapid forward swimming of the host cetacean, currents that might otherwise dislodge the amphipod form its flattened ectoparasitic position on the whale's skin

By contrast, basal and ischial lobes are apparently little developed within the mainly marine superfamily Hadzioidea, or in the mainly freshwater superfamilies Gammaroidea and Crangonyctoidea, even in free-swimming species that possess powerfully subchelate male

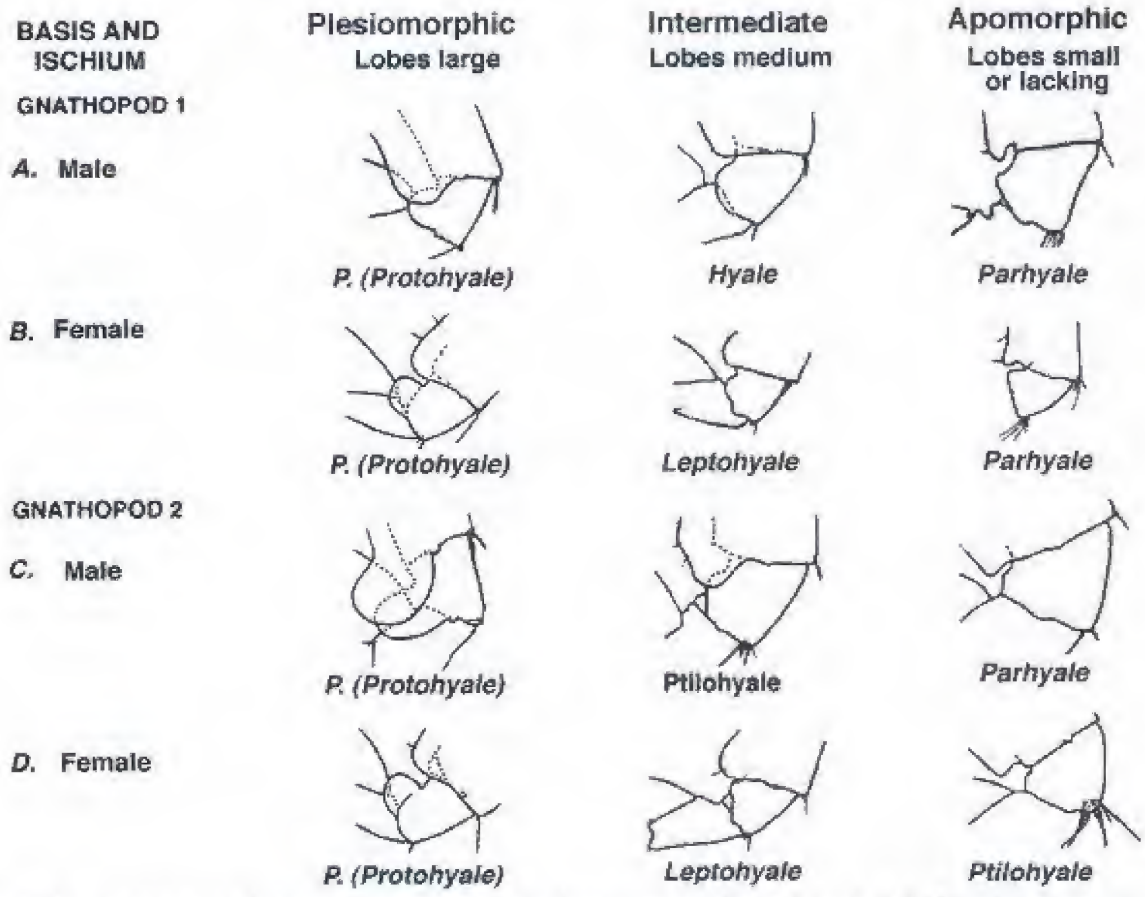

Fig. 4 Hydrodynamic lobes of basal and ischial segments of gnathpods 1 & 2 (lateral view) in mature male and female hyalid amphipods: character states.

gnathopods, often of preamplexing function. Hydrodynamic lobes are also not well developed within most superfamilies of the "Natantia " taxonomic category, except in a few instances where gnathopods are powerfully developed and short-wristed (e.g., *Eusiroides diplonyx* Barnard 1970).

The balance of morphological evidence, mainly within superfamily Talitroidea, indicates that basal and ischial lobes are best developed in powerfully subchelate gnathopods which fold tightly into a streamlined (hydrodynamic) swimming position, presumably during preamplexing "carrying" of the female. Exceptions to such generalized observations, especially among non-talitroidean amphipods, suggest that full solution to their functionality may require rigorous observations and high-speed photography of swimming amphipods under controlled laboratory conditions.

2. The posterior marginal cusp of coxae 1-4.

The posterior margin of coxal plates 1-4 frequently bears a median short sharply rounded thumb-like process or acclivity (Barnard 1979), here termed the posterior marginal cusp (figs. 1E, 2F). The cusp occurs on all four coxal plates of species of advanced saltatory genera (e.g., *Apohyale*, *Ptilohyale*) within family Hyalidae and most species of family Talitridae (except some sandhoppers). The cusps are limited to fewer coxae, or none, in mainly aquatic hyalids and are absent from other families within the Talitroidea.

The function of the cusp has not been determined precisely. Its presence mainly in saltatory species suggests that, during a jumping or springing action, the cusp prevents hyperspreading of the plates beyond mechanically safe limits and thus ensures that adjacent plates return to their properly overlapped deflexed positions on termination of saltation.

In some primitive saltatory groups (e.g., *Parhyale*), a distinct cusp may be lacking but a postero-distal shelf is usually present. The shelf may be sharply rounded or shallow and nearly straight or imperceptible, especially on coxa 1 (e.g., in *Hyale* spp., Fig. 46). In *Parhyale*, short blunt cusps are usually present on the broad posterior shelf of coxae 2 & 3, but coxa 1 bears a narrow shelf only. Also in *Parhyale*, and some species of *Protohyale*, the proximal posterior margin typically bears a broadly obtuse cusp about mid point.

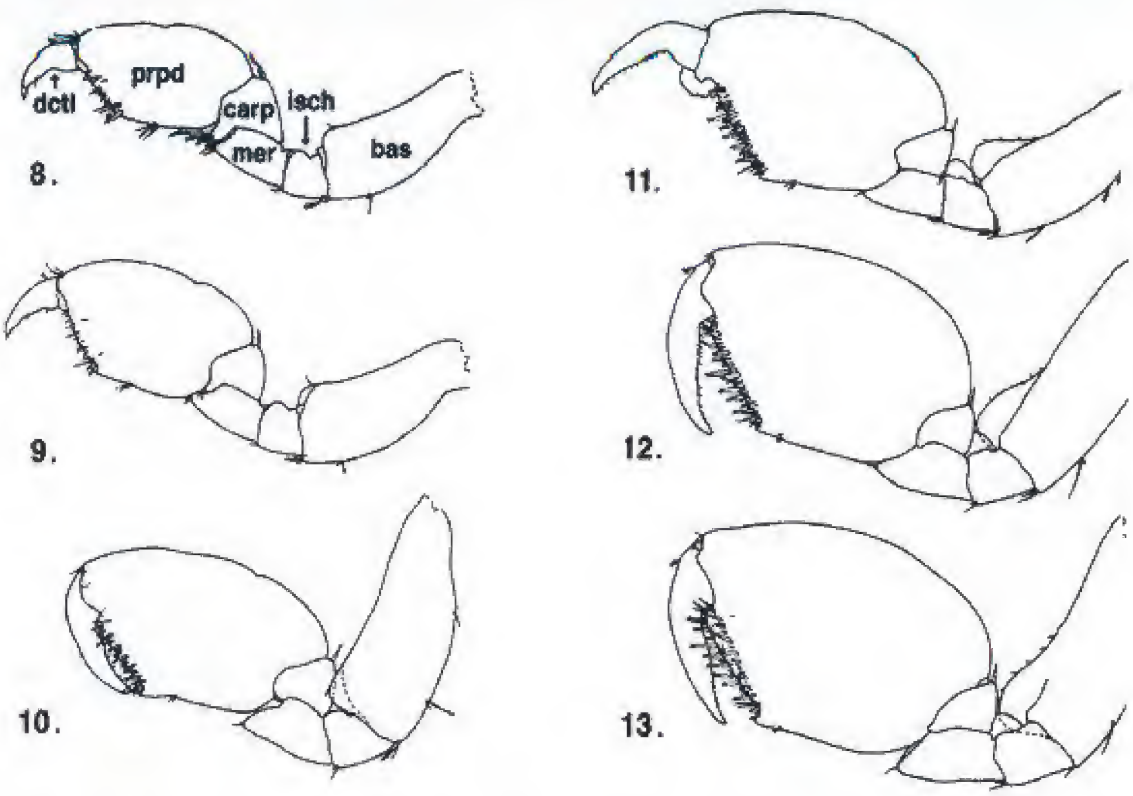

Fig. 5. Final 6 stages (Nos. 8-13) of development of gnathopod 2 in the male of *Protohyale (P.) media* (Dana) (medial view) (modified from Leite & Wakabara 1989).

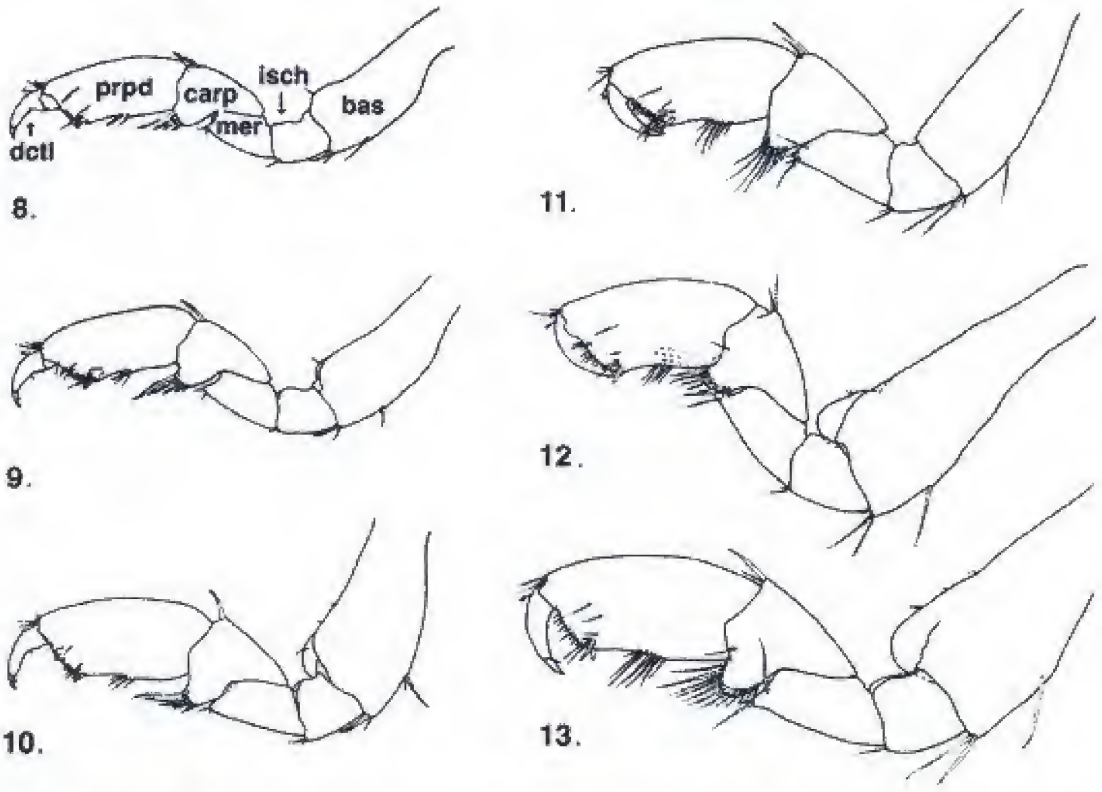

Fig. 6. Final 6 stages (nos. 8-13) of development of gnathopod 2 in the female of *Protohyale (P.) media* (Dana) (medial view) (modified from Leite & Wakabara 1989).

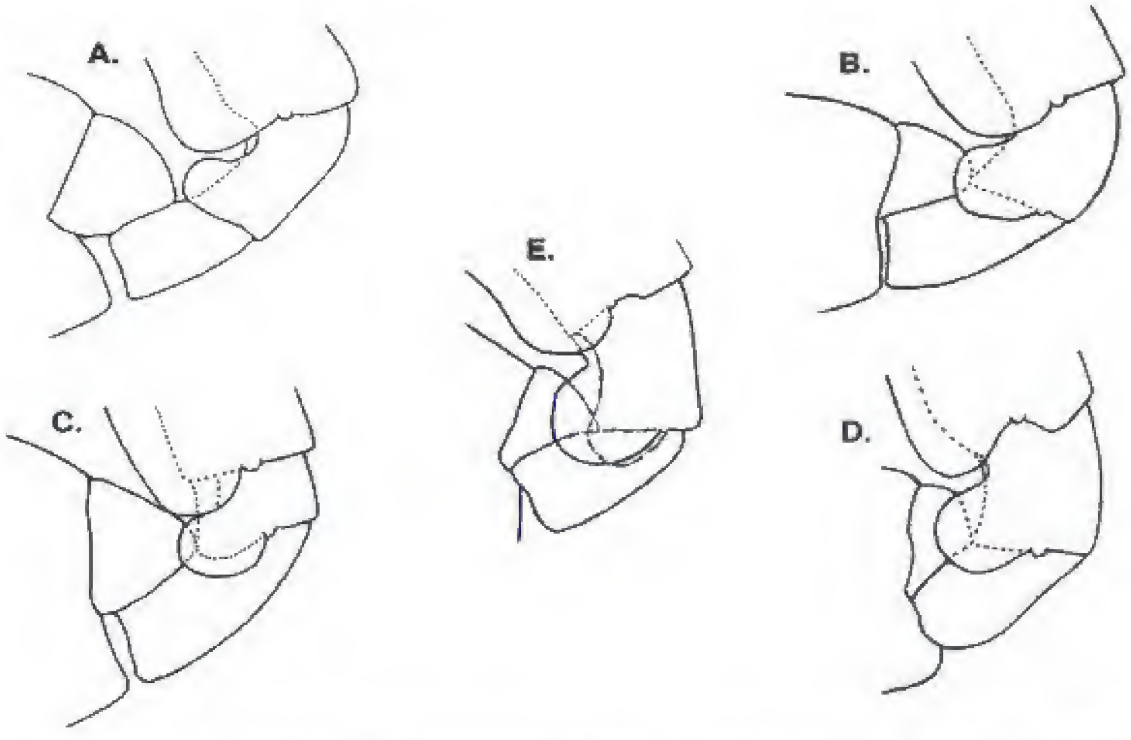

Fig. 7. Hydrodynamic lobes of basis and ischium of gnathopod 2 (male) in genera of palustral Talitridae. A. *Protorchestia* sp. male (8.0 mm). Heathcote, New Zealand. B. *Parorchestia rectipalma* (K. H. Barnard); male (9.0 mm), Port St. John, S. Africa. C. *Parorchestia tenuis* (Dana); male (8.6 mm); South Island, New Zealand. D. *Uhlorchestia uhleri* (Shoemaker); male (10.0 mm); Suwanee estuary, Florida. E. *Chiltonorchestia* sp. male (15.0 mm); west of Paita, New Caledonia. (Lateral view illustrations, based on material and slide mounts in crustacean collections of the Canadian Museum of Nature, Ottawa).

3. The peraeopodal notch and "surge seta"

Taxonomic illustrations of the posterior margin of the broadly expanded bases of peraeopods 5-7 of hyalid amphipods frequently include a single small but distinct indentation or "notch" in which sits a short thick distally tufted seta (e.g., Hurley 1957; Barnard 1974, 1979). In hyalid material from the Ryukyu Archipelago, Hirayama (1980) described the posterior basal margins of peraeopods 5-7 as "having small concavity with one plumose seta", but little detail is provided there or previously. This seta may protrude slightly further than the regular marginal setae (Fig. 8). The flexible setal stalk increases slightly in thickness distally, and its length is about 5-6X its average width. Its apical crown of 6-10 tendril-like filaments provides an overall superficial ressemblance to a miniature *Hydra*. The seta and notch occur mainly on margins that are crenulated, and are usually weak or lacking on those that are smooth or weakly denticulate (Figs. 9,10).

The function of this single specialized seta has not been determined experimentally, and is presently enigmatical. The posteriorly overlapping and broadened bases of peraeopods 5-7 form, in effect, a hydrodynamic continuation of the anteriorly overlapping broadened coxae 1-4 that "streamline" the sides of the body for forward swimming (Boudrias 1991). The specialized seta, about midpoint along the trailing edge of the basal plate, would seem well positioned for sensing the speed and direction of laminar water flow over the body surface. The present appellation "surge seta" is therefore possibly functionally descriptive.

In species that are mainly intertidal in vertical station and/or saltatory in behaviour (e.g., in *Ptilohyale, Apohyale*), or hypogean (e.g., in *Ruffohyale*), the surge seta may be weakly developed, present in one or two peraeopods only, or entirely lacking. The surge seta is weak in genus *Parhyale* and absent in freshwater species (e.g., in *Hyalella* of family Hyalellidae),

In males, the notch appears deeper and the seta is slightly stronger, with more apical filments, than in females (Fig. 9). The setal notch tends to be deeper, and the seta more strongly developed, with more apical filaments, in natatory genera (e.g., *Protohyale*, Fig. 8) than in saltatory genera (e.g., *Ptilohyale* and *Apohyale*, Fig. 9 & 10).

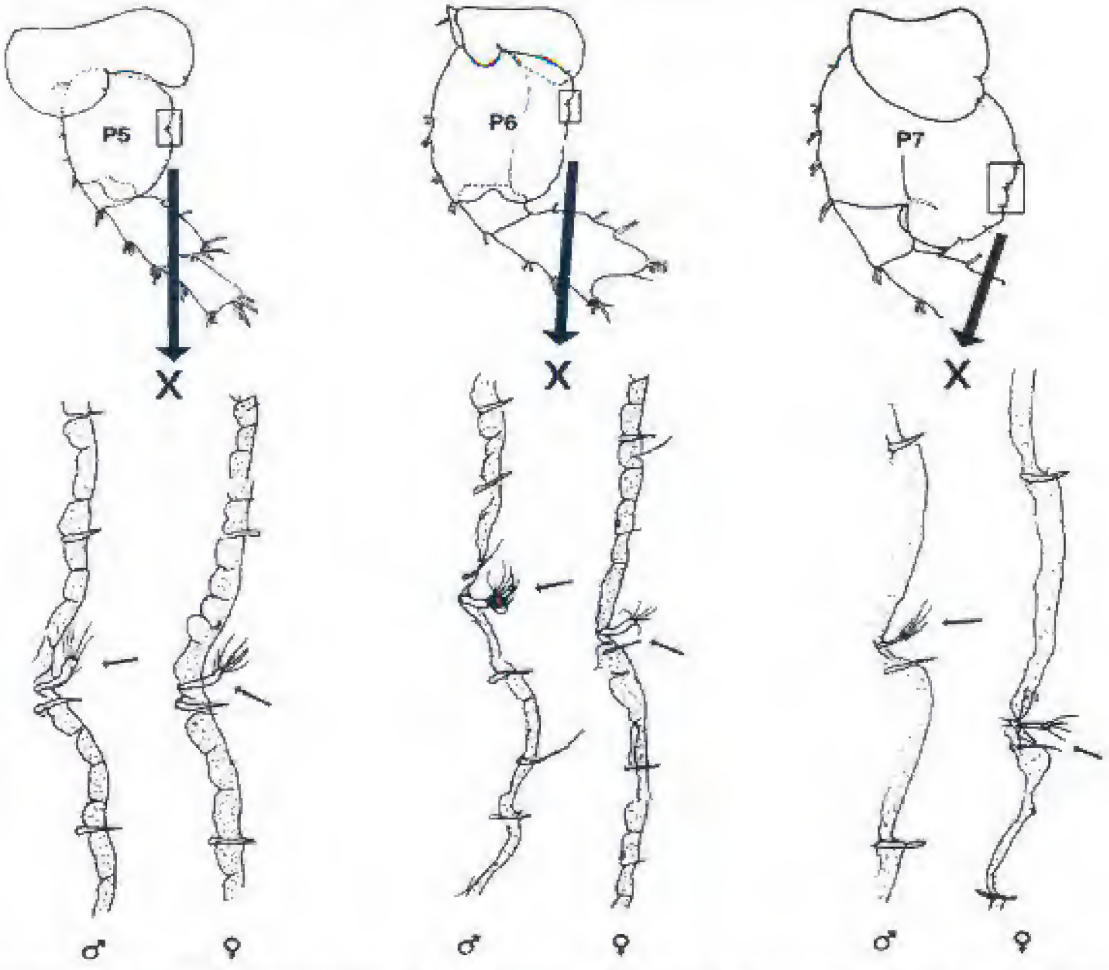

Fig. 8. Portion of the posterior margin of the bases of peraeopods 5-7 showing notch and surge seta. *Protohyale* sp. (= *P. dollfusi* Hiwatari) Ozuski, Japan. Male (5.5 mm); female ov (4.5 mm?) (X40).
Note: Insets showing portions of representative peraeopods 5-7 after Hirayama (1980).

4. The Interlocking brood plate.

Virtually unique among gammaridean amphipods are the interlocking female brood plates of several talitroidean families (Figs 11, 12). Although the four brood lamellae are very seldom illustrated in taxonomic accounts , that of peraeopod 2 (gnathopod 2) is the most frequently shown and is therefore utilized in group comparisons here.

In fully aquatic (primitive) species of Hyalidae (e.g, in *Parallorchestes* and *Protohyale* (sens. lat), the brood lamellae are typically broadly ovate in outline, narrowing gradually distally and bluntly or broadly rounded apically (Figs. 11 A-D; 12 E-F). The numerous (60-100+) close-set marginal setae are nearly uniformly elongate, mostly greater than half the width of the plate. The setal tips are invariably hook- or crook-shaped (Fig.12, inset), although some published illustrations do not show that detail. During gestation of eggs and protection of newly hatched young in the brood pouch each seta apparently interlocks with a counterpart seta of an adjacent brood plate. All brood plates (peraeopods 2-5) are similarly subovate or elongate ovate, with rounded apices and elongate marginal setae (Figs. 12 E, F). The interlocking setae presumably function in preventing separation of the plates and spilling of the brood contents during rigorous tumbling action of highly lotic aquatic environments such as the surf zone and/or during active saltation by intertidal species in the air medium. In aquatic species, the copious spaces between the interlocking setae presumably facilitate direct interchange (flushing) of brood pouch fluids with the surrounding salt-water medium. Yet unknown is a mechanism by which the setae "unlock" to permit spreading of the plates and egress of the newly hatched young, and also return of those early instars to the temporary protection of the pouch (Fig. 13D)*.

In somewhat more advanced "intermediate" hyalid genera such as *Hyale* and *Ruffohyale* and some species within subgenus *Protohyale* (Figs. 11 F), the plate itself becomes longer and the apex more sharply rounded, the individual setae are shorter, and the pouch presumably

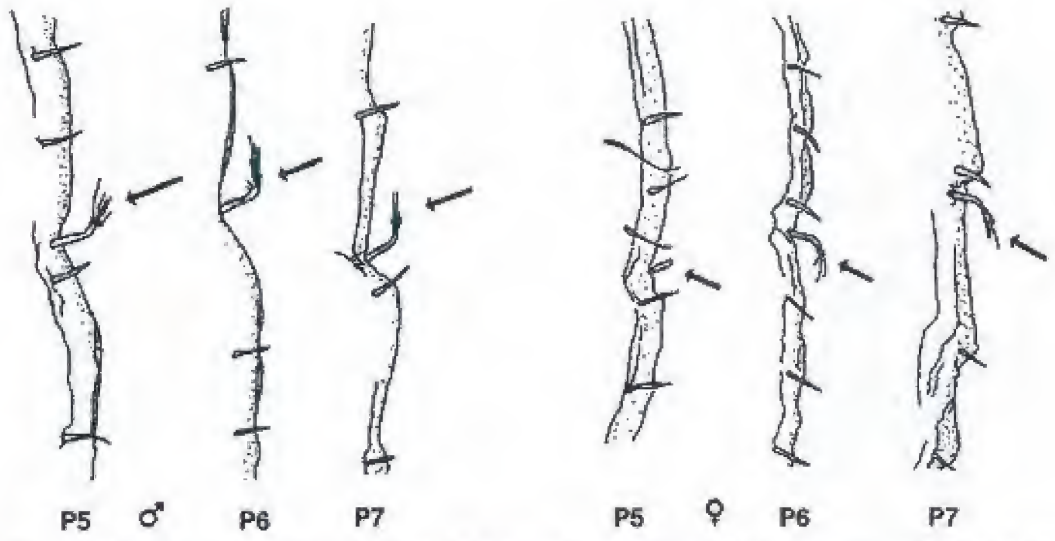

Fig. 9. Portion of the posterior margin of the bases of peraeopods 5-7 showing notch and surge seta. *Ptilohyale barbicornis* Hiwatari & Kajihara,1981b. A. Male (9 mm); B. female ov (5.0 mm).Tokyo Bay.

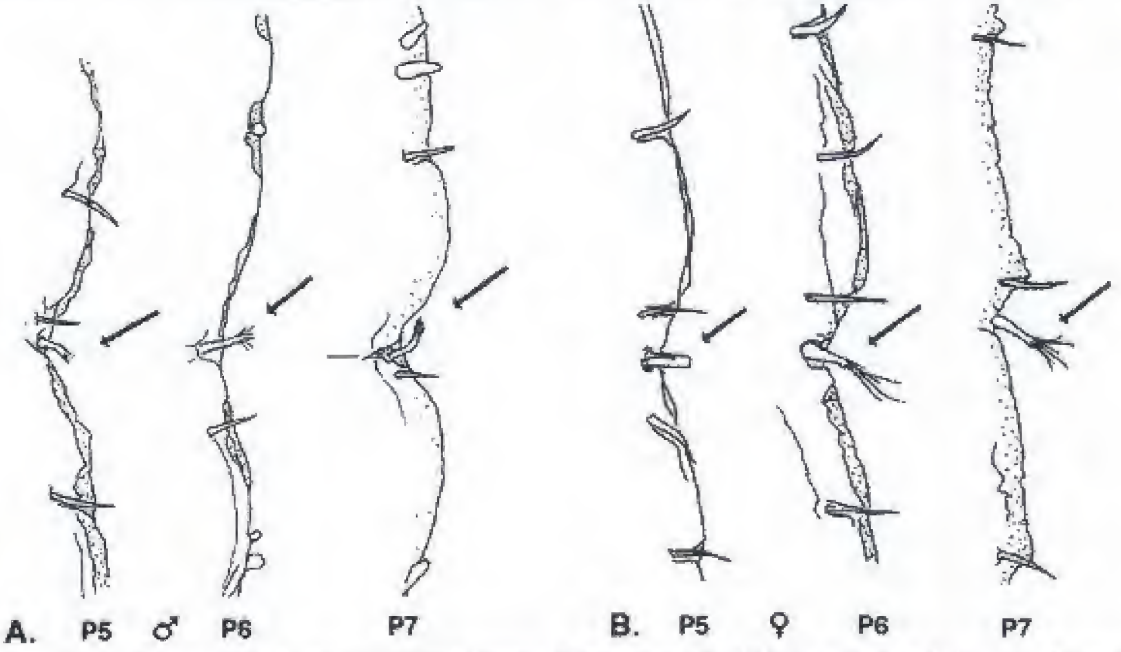

Fig. 10. Portion of the posterior margin of the bases of peraeopods 5-7 showing notch and surge seta. *A. Apohyale honoluluensis* (Schell.). Male (6.0 mm), Asari, India. B. *Apohyale punctata* Hiwatari & Kasihara, 1981b. Male (9.0 mm), Natsushima, Japan.

more tightly closed to interchange with the external medium.

In the most advanced genera (e.g., *Ptilohyale, Apohyale*, and *Serejohyale*), component species exist partly or entirely intertidally. With increasing terrestriality of the species, the brood plates tend to show a corresponding increase in overall size (in length and/or width), a more sharply acute apex, and the individual marginal setae tend to be very short, closely set, and presumably very tightly interlocking (Fig. 12C). The primitive oval shape of the P2 and P5 plates becomes secondarily broadly triangular, and that of P3 and P4 middle plates subrectangular or rhomboidal (Figs.12E, F). Such trends may also be noted in corresponding brood plates within the closely related family Hyalellidae, and its offshoot fossorial family Dogielinotidae, endemic to the North Pacific region (Figs. 12B, D; 13A-D). Such conforms with a large brood pouch that is tightly closed to interchange with the external medium (Fig. 13D). In intertidal species, tightly closed brood pouches presumably protect the developing eggs from sudden osmotic changes caused by exposed to the freshwater of rain and stream flow. The similarly "tight" brood pouches of freshwater Hyalellidae (esp. the Chiltoniinae) presumably maintain an osmotically stable osmotic environment for the devel-

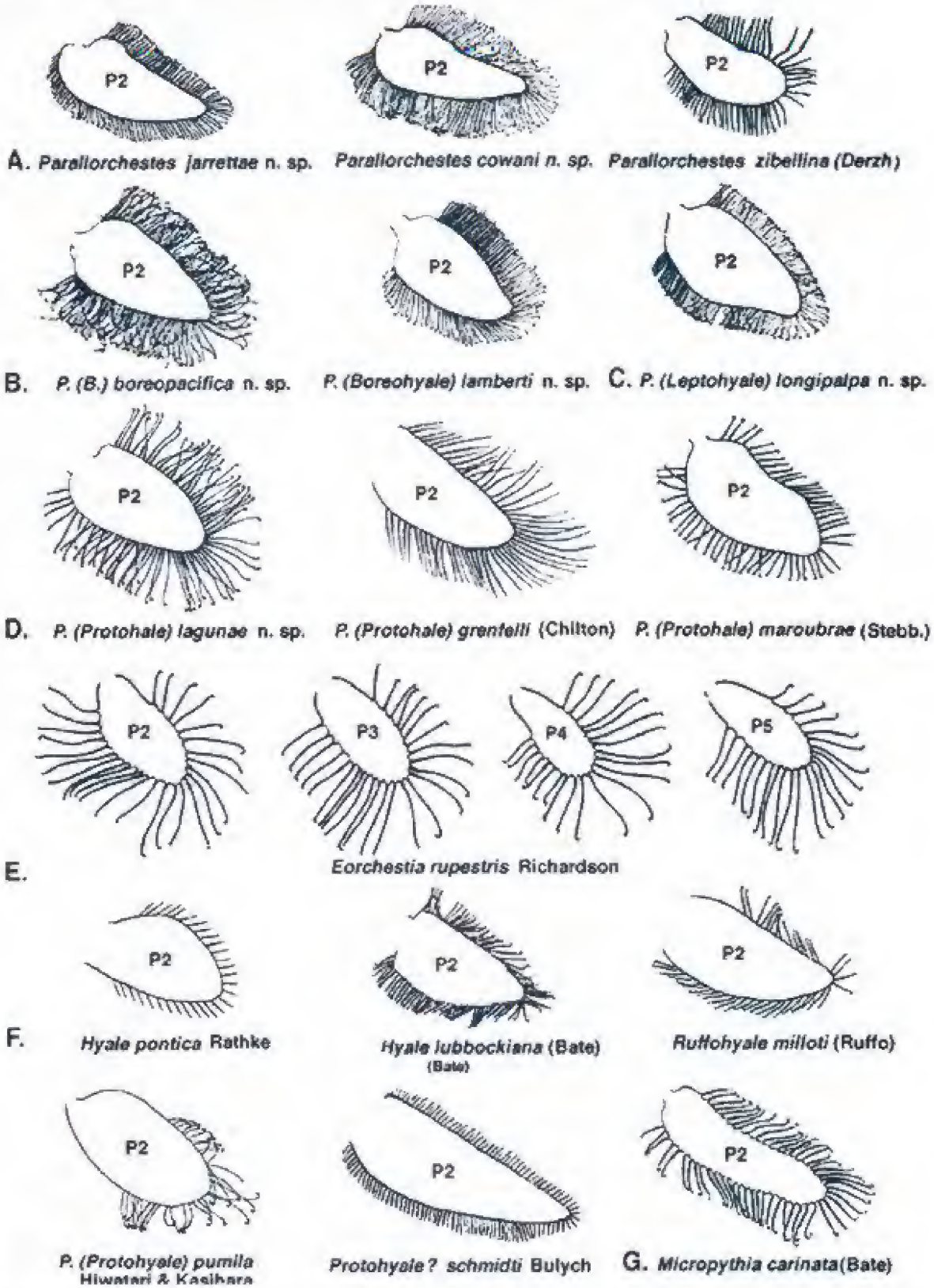

Fig. 11. Brood lamellae of representative primitive and intermediate genera of Hyalinae, subfamily Kuriinae and a palustral species of Talitridae. A. *Parallorchestes*; B. *Protohyale (Boreohyale)*; C. *P. (Leptohyale)*; D. *P. (Protohyale)*; E. Palustral Talitridae; F. Intermediate genera of Hyalinae; G. Kuriinae. Illustration modified from A. Derzhavin (1937); D. Hurley (1957);E. Richardson et al. (2001), F. Hiwatari & Kajihara (1981a), Bulycheva (1957), Ruffo (1958), Krapp-Schickel (1993). Other illustrations original in this paper.

oping eggs, perhaps aided by the osmoregulatory sternal gills (Figs. 13A-D). The close similarity of brood plates of *Austrochiltonia* with those of *Hyalella* (Fig. 12D), and dissimilarity with those of *Ceina* and *Tahaipe* (Figs. 13 E,F) further supports recent classification of the Chiltoniinae within family Hyalellidae rather than family Ceinidae (Bousfield 1996; Hendrycks and Bousfield 2001).

Extreme attenuation and "distortion" of outline have been described in all four brood lamellae of *Hyachelia tortugae* (Hyacheliinae), epiparasitic in the buccal cavity of marine turtles (Fig. 12 G, Barnard 1967). Speculation on pathways and timing of its evolution, possibly from an *Apohyale* or *Serejohyale*-like progenitor, in concert with the morphological evolution, and development of migration patterns of the Atlantic host turtle species, remains moot.

Consideration of hyalid brood plate morphology may shed light on possible evolutionary pathways that gave rise to semi-terrestrial and terrestrial amphipods now classified within family Talitridae. Talitrids differ from hyalids mainly in the reduced size of antennae, mouthpart palps, and coxa 1, in fusion of the telson lobes, and in the specialized "mitten"-like form of gnathood 2 of all female talitrids, perhaps the most significant in terms of effect on life style and behaviour. Because of mostly relatively slight morphological differences, the saltating terrestrial talitrid amphipod may have evolved from a semi-terrestrial (intertidal) saltating hyalid (Duncan 1985). Modern aquatic hyalids might also be secondarily derived from intertidal hyalids.

However, Richardson et al. (2001) noted that increasing terrestriality in the Talitridae was marked by decrease in size of brood lamellae, reduction in extent of marginal setae, loss of terminal hooks on the setae, and general "opening" of the brood plates. Morpholgical difference may be at least partly attributable to the relatively large clutch sizes and small size of eggs of intertidal hyalids, versus the relatively small clutch sizes and relatively large eggs of palustral and intertidal talitrids. The brood lamellae of those primitive semiaquatic and presumed ancestral Talitridae (e.g., *Eorchestia rupestris*, Fig. 11E) are broadly ovate, with rounded apices and long hook-tipped setae, little different in appearance from those of aquatic hyalids (e.g., *Parallorchestes* and *Protohyale)* (Fig. 11 A-D). They contrast sharply with the elongate, broadly spade-shaped, brood lamellae lined with numerous, closely set, short setae in the advanced saltatory intertidal hyalids (Fig. 12 E,F). The latter would seem an unlikely ancestral condition for either aquatic members of Hyalidae or for primitively aquatic members of family Talitridae. Thus, on the basis of brood plate morphology,the ancestral talitrid was more likely to have been an aquatic rather than semi-terrestrial hyalid.

Paradoxically, increasing size and "tightness" of the brood pouch in semiterrestrial hyalid amphipods (e.g., *Apohyale pugettensis*) more closely parallels that of oniscoidean isopods, the terrestrial females of which carry large numbers of relatively small eggs in the thoracic brood pouch (Heeley 1941). The young (first two instars) of *Parallorchestes ochotensis* may seek extended postnatal protection from predation in the female brood pouch (Kobayashi et al. 2002). While in the pouch the young are able to feed on seaweed closely pressed to the underside by the mother animal, and also moult during this period. However, egress and return to the brood pouch has been observed under artificial laboratory conditions, apparently unimpeded by mechanical interlocking of the relatively elongate and flexible brood setae.

Within modern saltating intertidal hyalid genera (e.g., *Ptilohyale, Apohyale*,and *Serejohyale*) the specialized form of brood lamellae may represent, at least in part, a morphological-behavioural adaptation to ensuring safe retention of large numbers of relatively small eggs within the brood pouch. Their newly emerged instars may be barred from ready return to the shelter of such a pouch (e.g., in *Apohyale pugettensis*) but alternatively take shelter under the shells of intertidal limpets (Johnson 1968). Such action may also protect the juveniles from potentially lethal osmotic changes during heavy rainfall at ebbtide.

5. The preamplexing notch*

Observations on precopulatory and mating behaviour in talitroidean amphipods were pioneered by Borowsky (1984), furthered by Conlan (1991), and Bousfield and Shih (1994). During precopulatory behaviour of hyalellid amphipods , the male "rides" or "carries" the female in dorsal position. The dactyl of gnathopod 1 is inserted in a morphological indentation or "notch" in the anterodistal margin of peraeon segment 2 of the receptive mature female. The morphology of the preamplexing (precopulatory) notch has been described and figured in several genera and species within talitroidean family Hyalellidae (Hendrycks & Bousfield 2001). The notch is here found nearly

* superficially similar hook-tipped brood setae occur in females of some members of corophioidean family Ampithoidae.

*SEM enlargments are not yet available, so the ultrastructure of the notch is unknown).

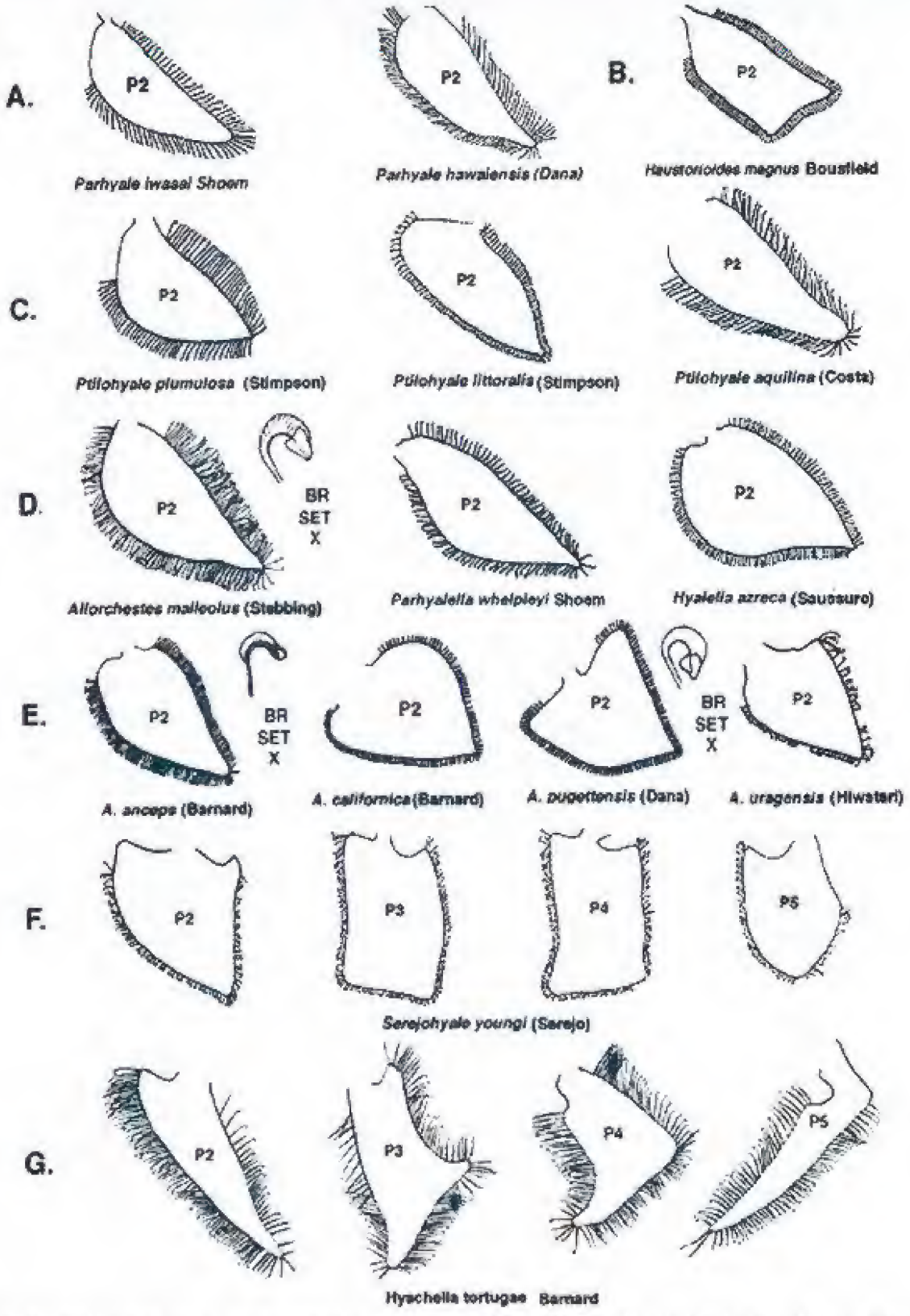

Fig. 12. Brood lamellae of representative genera of Hyalellidae, Dogielinotidae, Hyacheliinae, and advanced genera within subfamily Hyalinae. A. *Parhyale;* B. Dogielinotidae; C. *Ptilohyale;* D. Hyalellidae; E. *Apohyale*; F. *Serejohyale*; G. Hyacheliinae. Illustrations modified from: A. Bulycheva 1957, Shoemaker 1956; B. Bousfield & Tzvetkova 1982; C. Bousfield 1973, Krapp-Schickel 1993; D. Hendrycks & Bousfield 2001; E. Hiwatari & Kajihara 1981a; F. Serejo 2001; G. Barnard 1967. Other illustrations original in this paper.

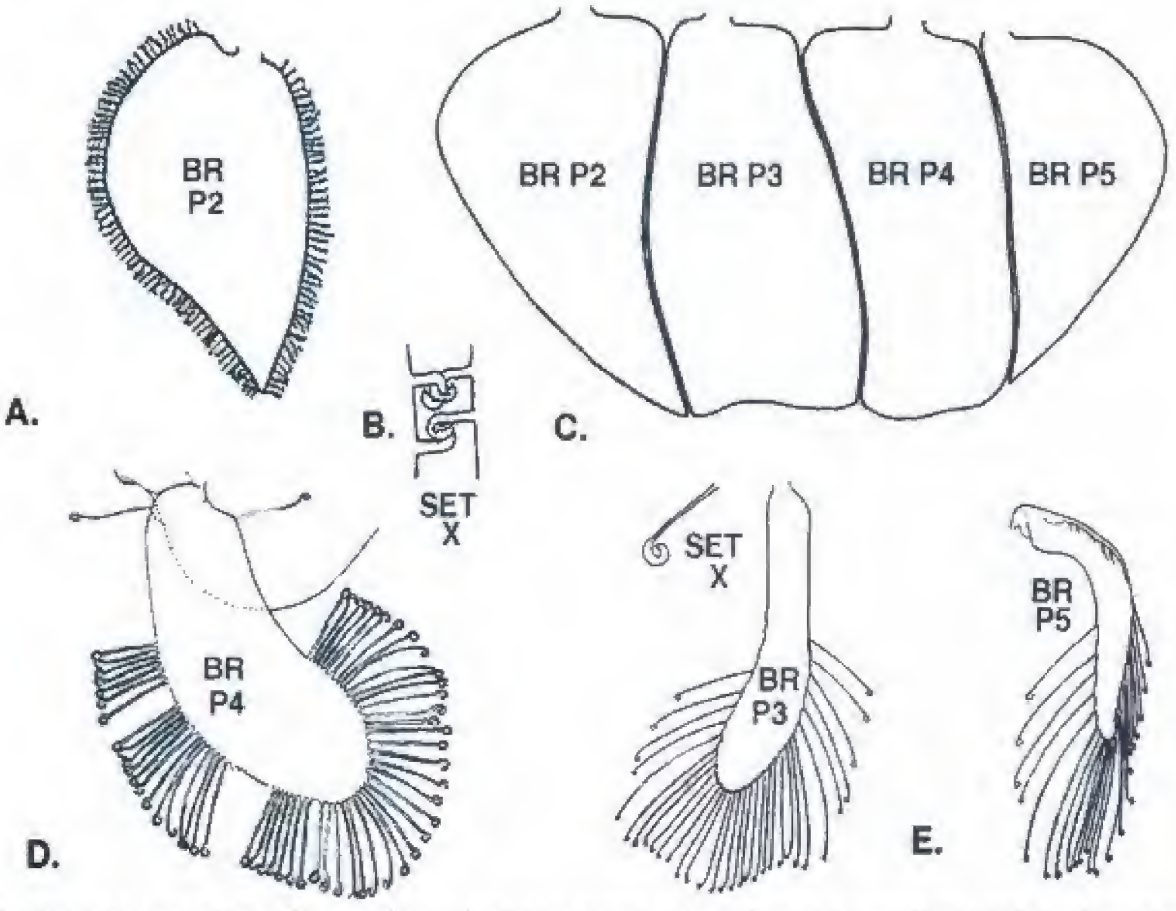

Fig. 13. Female brood lamellae and interlocking brood setae of aquatic and intertidal talitroidean amphipods. A, B, C: Hyalellidae D. E: Ceinidae *(Ceina egregia, Tahaipe karori)*. A, B:*Hyalella azteca,* British Columbia; C. *Austrolchiltonia* sp. 2, Hatfield R., Tasmania. Lateral view reconstruction of brood lamellae forming brood pouch (Figs. A-C drawn from CMN material and slide mounts; D, E,. modifed from Barnard 1972).

universally within sexually mature and/or egg-bearing females of family Hyalidae (Figs. 14, 15) including *Hyachelia tortugae,* ectoparasitic on marine turtles, and in all genera and species of the North Pacific family Dogielinotidae (Fig. 14D). However, the notch has not been found in males nor in subadult females and immature stages of the above families and genera. The notch has not yet been found in mature females of other talitroidean families including Talitridae (e.g., *Eorchestia, Protorchestia*), Najnidae, Phliantidae, Temnophliantidae, Ceinidae, or subfamily Chiltoniinae within Hyalellidae (e.g., in *Austrochiltonia, Afrochiltonia*).

Within family Hyalidae, the notch appears to follow a phyletic pattern (Fig. 14A) that parallels the phylogeny of other phyletically significant characters states, including those of the gnathopods, coxal plates, uropods, and telson (Figs. 1, 2, 3). Thus in relatively primitive genera (e.g., *Parallorchestes, Parhyale*) the notch is usually a shallow indentation in a slightly ventrally extended anterior lower lobe of peraeon segment 2 of the female. In a more advanced condition, as in *Apohyale* and *Serejohyale*, the notch is deeper and sharply rounded, and the lower peraeonal lobe deeper. In the most advanced family condition, as in *Protohyale* and *Ptilohyale*, the notch is deeply indented and the inner angle is narrowly produced inwards as a long slender groove, usually at an angle to the body axis, termed the unguisial groove (Hendrycks & Bousfield, 2001). The posterior peraeonal lobe is usually deep, with rounded anterior margin. In the most advanced genus (*Hyale*) an accessory "locking slit" is located immediately above the lower margin of the anterior peraeonal lobe, presumably into which fits the propodal "guiding spine" of the male gnathopod 1. Similarly, in some species of *Allorchestes* (within family Hyalellidae), the facial locking spine of the propod of gnathopod 1 (♂) presumably fits into a secondary facial groove of peraeon 2 of the female, termed the locking slit.

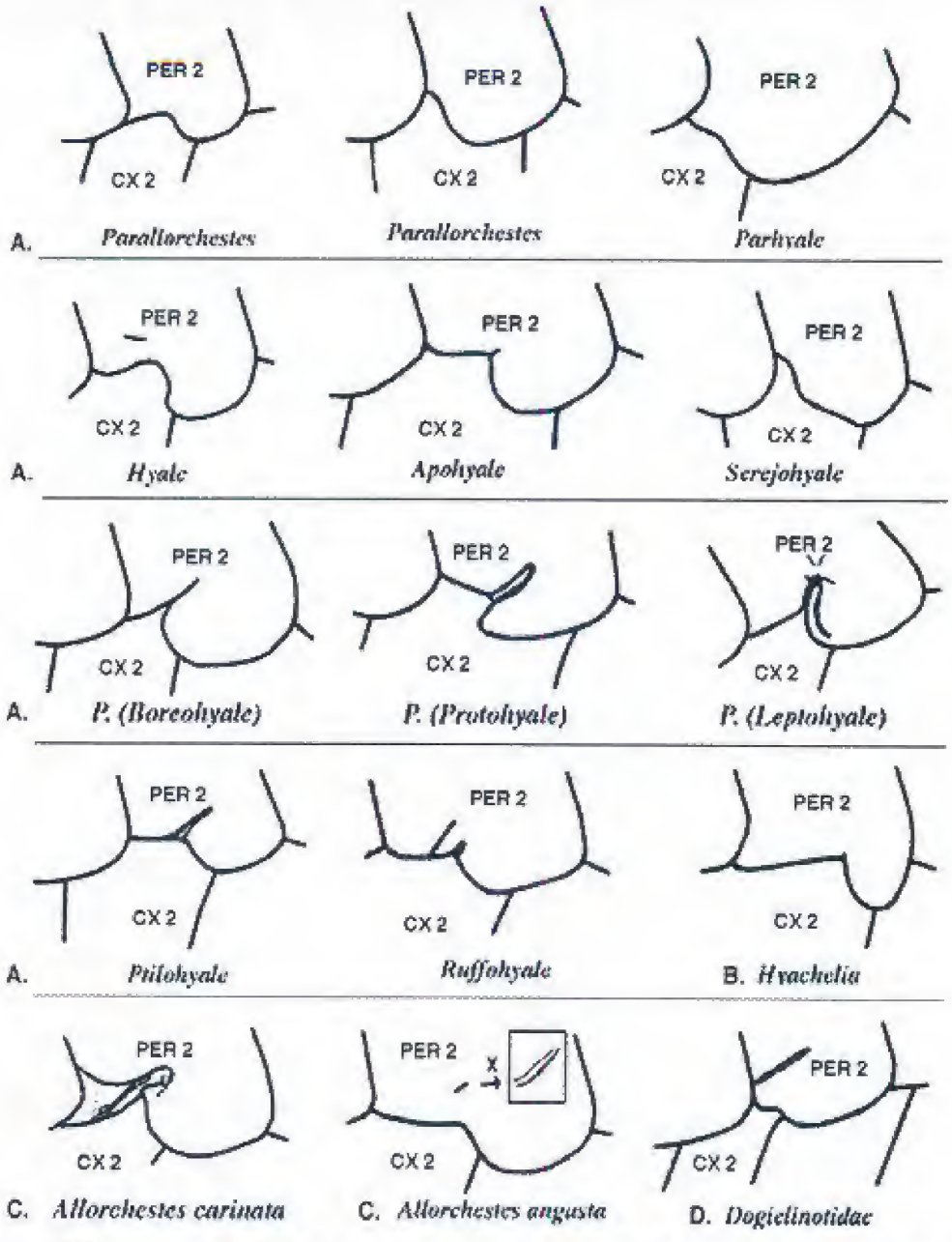

Fig. 14. Form of the pre-amplexing notch of mature females within genera of families and subfamilies of superfamily Talitroidea. A. Hyalinae B. Hyachelinae C. Hyalellidae D. Dogielinotidae.

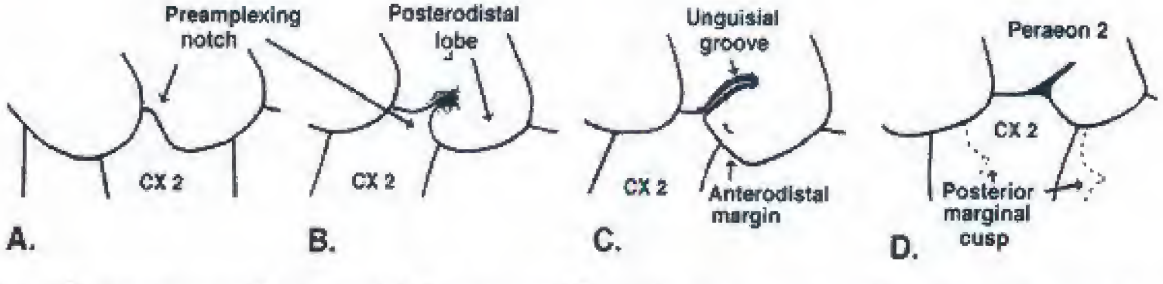

Fig. 15. The preamplexing notch in western North Pacific species of Hyalidae: Terminology. A. *Parallorchestes zibellina* (Derzhavin, 1937); B. *Protohyale (P.) pseudopumila* (Hiwatari & Kajihara, 1981a); C. *Protohyale (P.) hololuluensis* (Schellenberg, 1938); D. *Ptilohyale barbicornis* (Hiwatari & Kajihara, 1981b). (illustrated from CMN collections).

KEY TO WORLD GENERA OF HYALINAE (excluding *Neobule* Haswell*)

(Figure symbols: a = apomorphic; i = intermediate; p = plesiomorphic

1. Peraeopods 3-7, dactyls medium to large (1/4-1/2 propod), inner marginal seta of dactyl very small or lacking (fig. 2Ep); clasping spine of segment 6 usually strong (fig. 2Da); coxa 1 lacking cusp or shelf (Fig. 1Ep). . . 2.
Peraeopods 3-7, dactyls small (<1/4 propod), inner marginal seta distinct; clasping spine of segment 6 small or lacking; coxa 1 with posterior marginal cusp or shelf . . . . 7.

2. Coxae 2 and 3 with posterior marginal cusp (Fig. 1Ea); uropod 1, peduncle with weak distal spines (Fig. 3Aa); gnathopod 1 (♂), propod with stout medio facial guiding spine (fig. 2Ba) . . . . *Hyale* Rathke (p. 93)
Coxa 2 and 3 lacking posterior marginal cusp; uropod 1, peduncle with stout distolateral spine; gnathopod 1 (♂); propod lacking stout medio facial guiding spine . . . . 3.

3. Gnathopod 2 (♂), carpal lobe prominent (Fig 2Cp); uropod 3 biramous (inner ramus small, distinct (Fig. 3Bp;) telson lobes each with apical spine (s) (Fig. 3Cp); maxilla 1 palp 2-segmented, proximal segment short (Fig. 1Cp) . . . . *Parallorchestes* Shoemaker (p. 36)
Gnathopod 2 (♂), carpal lobe lacking or vestigial; uropod 3 uniramous (or inner ramus fused to peduncle); telson lobes, apical margin smooth, unarmed; maxilla 1, palp 1-segmented or with median constriction. . . . 4.

4. Gnathopod 1 (♂), dactyl strongly bidentate (Fig. 2Bp); maxilliped palp (♂), unguis normal (Fig. 1Dp) . . . . ***Protohyale* (*Dipolohyale*)** n. g., n. subg. (p. 90)
Gnathopod 1 (♂), dactyl simple(unguis rarly bifid); maxilliped palp (♂), unguis often elongate, whip-like. . 5.

5. Peraeopods 5 and 6, segment 4 strongly broadened (width > length)(Fig. 2Fa) . . . . . . *Lelehua* Barnard (p. 92)
Peraeopods 5 and 6, segment 4 normal or slightly broadened (length >width) . . . . 6.

6. Antenna 1 peduncle 2 short, little longer than 3; gnathopod 1 (male), basal and ischial lohydrodynamic lobes strongly developed. . . . . ***Protohyale (Protohyale)*** n.g., nom. subg. (p. 79)
Antenna 1, peduncle 2 distinctly longer than 3; gnathopod 1, basal and ischial lobes weakly or not developed in males and females.. . . . . ***Protohyale* (*Boreohyale*)** n. g., n. subg. (p. 61)

7. Uropod 1, peduncle with strong distolateral and/or distomedial spines Fig. 3Ap). . . . . 8.
Uropod 1, distal spines of peduncle small, weak . . . . 11.

8. Antenna 2, flagellum and peduncular segment 5 strongly plumose-setose (both sexes) (Fig. 3Aa); uropod 1, peduncle with strong distomedial spine only (Fig. 2Dp); gnathopod 2 (♂), carpal lobe usually present, small (Fig. 2Fi); inner ramus of uropod 3 variously fused to peduncle (Fig. 3Bi) . . . . ***Ptilohyale*** n. g. (p. 98)
Antenna 2, flagellum and peduncular segment 5 unarmed, weakly setose, or setae also present on peduncular segment 4; uropod 1, peduncle with strong distolateral and distomedial spines, or distolateral spine only; gnathopod 2 (♂), carpal lobe usually lacking or vestigial; inner ramus of uropod 3 either distinct, or lacking totally . . . . 9.

9. Uropod 1, peduncle with stout distolateral and distomedial spines (Fig. 3Ai); coxae2 and 3 with strong posterior marginal cusps (Fig. 1Ea) . . . . ***Serejohyale*** n. g. (p. 114)
Uropod 1, peduncle with distallateral spine only; coxae 2 and 3 with shelf but lacking cusp . . . . 10.

10. Uropod 3 biramous, inner ramus very small (Fig. 3Bp); coxa 4 with broad cusp on posterior excavational margin (Fig. 2Aa); mandible, left lacinia 5-dentate Ffig. 1Bp); maxilliped palp (♂) normal (Fig. 1Dp) . . . . *Parhyale* Stebbing (p. 96)
Uropod 3 uniramous; coxa 4 lacking posterior marginal cusp; mandible, left lacinia 7-dentate; maxilliped palp (♂), dactyl elongate . . . . ***Protohyale (Leptohyale)*** n. g., n. subg. (p. 88)

11. Pigmented eyes lacking; brood plate (peraeopod 2) apically rounded, marginal hooked setae medium long (Fig. 3Di); in hypogean fresh waters . . . . ***Ruffohyale*** n. g. (p. 116)
Pigmented eyes present, usually large (fig. 1Aa); brood plate (peraeopod 2) large, broad, apex acute, marginal setae short, numerous(Fig. 3Da); marine intertidal . . . . ***Apohyale*** n. g. (p. 104)

**Neobule* Haswell: most characters and character states are imprecisely known (see Barnard & Karaman 1991)

Parallorchestes Shoemaker

Parallorchestes Shoemaker, 1941: 183;—Barnard 1952: 23;—Barnard 1962: 160;—Barnard 1979: 119;—Bousfield 1981: 75;—Barnard & Karaman 1991: 370;—Ishimaru 1994: 69.
Parhyale (part) Gurjanova 1951: 813;—Bulycheva 1957: 78;—Stock, 1987: 167.

Type species: *Allorchestes ochotensis* Brandt, 1851, original designation.

Species: ***Parallorchestes alaskensis*** n. sp.; *P. americana Bousfield, 1981*; ***P. carinata*** n. sp.; ***P. cowani*** n. sp.; ***P. kabati*** n. sp.; ***P. leblondi*** n. sp.; ***P. minima*** n. sp.; ***P. subcarinata*** n. sp.; ***P. nuda*** n. sp. ***P. trispinosa*** n. sp.
Western N. Pacific
P. ochotensis (Brandt, 1851), (Bering & Okhotsk Seas); *P. asiaticus* Tzvetkova, 1990 (Russian Pacific coast); *P. zibellina* (Derzhavin, 1937) (N. Sea of Japan)

Diagnosis: Male. Body generally stout, medium to large. Peraeonal and abdominal segments often posteriorly ridged or mid-dorsally carinate. Eyes medium, sub-ovate. Antennae medium, subequal (antenna 1 slightly shorter, exceeding peduncle of antenna 2); peduncles stout, flagella and peduncles often posteriorly setose.

Upper lip, epistome large. Lower lip regular. Mandible, left lacinia 5 (6) dentate; spine row with 2-3 blades. Maxilla 1, palp 2-segmented, proximal segment very short. Maxilla 2, inner plate with inner marginal plumose stout setae. Maxilliped regular; palp stout, dactyl large, lacking whip seta in male.

Coxal plates 1-4 regularly broad, deep; posterior marginal shelf weak or lacking, cusps lacking. Coxal plates 5 variably aequilobate, occasionally aequi- or anterolobate; coxa 6 and 7 posterolobate. Coxal gills large, plate-like, on peraeopods 2-6.

Gnathopod 1 ordinary, weakly sexually dimorphic; basis propod with 1-2 posterodistal spines, neither modifed as a mediofacial guiding spine; palm smooth, not excavate; dactyl rarely bifid, overlapping posterodistal angle. Gnathopod 2 strongly sexually dimorphic; hydrodynamic lobe of basis and ischium moderately to strongly developed, overlapping (except in carinated and ridged species); carpal lobe small but distinct; propod large, palm regular; dactyl simple, stout.

Peraeopods 3-4 stout, spinose, segment 6 often with inner distal marginal locking spine. Peraeopods 5-7 stout, homopodous; bases broad, posterior margin with well-developed notch and surge seta. Peraeopod 5 shortest; segment 4 often widened; segment 5 short; segment 6 often with stout anterodistal subterminal clasping spine; dactyls large, simple, inner marginal seta small or lacking. Peraeopod 7, basis mediodistally sharply incised.

Epimeral plates regular, 2 deepest, hind corners squared. Pleopods regular, natatory, rami longer than slender peduncles. Uropods 1 and 2, rami longer than peduncle, with marginal and apical spines; peduncle with distolateral spine. Uropod 3 biramous, inner ramus small, rounded, with apical seta; outer ramus longer than peduncle, with marginal and apical spines.

Telson, lobes short, wide, separated to base, apical margin with spine(s) and setae.

Female: Gnathopod 1, hydrodynamic lobe weak or lacking on basis, and/or lacking on ischium. Gnathopod 2 regular, similar to but larger than gnathopod 1; carpal lobe well developed. Brood lamellae large, rounded apically; marginal setae numerous, long, hook-tipped. Preamplexing notch simple, shallow, lacking unguisial groove.

Distribution: Actively swimming among or clinging to algae in the low intertidal and littoral zone, along cold temperate, surf-exposed rocky coasts of the North Pacific, from Bering Sea south to the northern Sea of Japan, and central California.

Remarks: Barnard & Karaman (1991) did not recognize most of the new species names proposed by Bousfield (1981). New patronyms are provided below. The genus here encompasses 7 phenetic-phyletic subgroups, distinguishable at or below the 75% level of morphological similarity, but appear relatively closely related, above the 50% level of similarity (phenogram, Fig. 62, p. 126).

Stock (1987) minimized character state differences between *Parallorchestes* Shoemaker and *Parhyale* Stebbing. He supported the opinions of Gurjanova (1951) and Bulycheva (1957) that only one genus, *Parhyale*, is needed. Barnard (1979) also did not separate the two genera in his artificial key to known species of *Parallorchestes* and *Parhyale*.

The present analysis confirms the generically comprehensive significance of the following differences as outlined in Table II.

Table II. Character state differences between *Parhyale* Stebbing, 1897 and *Parallorchestes* Shoemaker, 1941.

Character	Character State	
	Parallorchestes	*Parhyale*
Body carination	posterodorsal	lacking
Antennae	grossly subequal (A2 sl.> A1)	unequal (A2 >> A1)
Maxilla 1, palp	2-segmented	1-segmented
MD, left lacinia	5 (6) dentate	5-dentate
GN1 & 2 (♂), basis, hydrodynamiclobe	large, rounded	small, subacute
GN2 (mature ♂), carpal lobe	present	lacking
Coxae 1-4	shelf weak,	shelf present, weak cusp
Coxa 4, cusp on posterior excavation	lacking	prominent
Peraeopods 3-7, dactyl type	large, ant.marg. setae minute	small, ant. marg. seta large
P5-7, basis, surge seta & notch	present, strong	lacking
Uropod 2, length of rami	unequal	subequal
Telson lobes, apical margin	apical spine(s) & setae	bare
Brood setae, length relative to brood plate width	elongate, setae >1/2 platewidth	short, setae <1/2 plate width
Distribution	boreal North Pacific	tropical-warm-temperate

Parallorchestes ochotensis (Brandt)
(Fig. 16)

Allorchestes ochotensis Brandt, 1851:143, pl. 6, fig. 27a-f.;—Holmes 1904: 233, fig. 118.
Hyale ochotensis Stebbing 1888: 247;—Stebbing 1906: 561.
Parhyale kurilensis Iwasa, 1934: 1, Pl. 1-II, fig. 1;—Iwasa 1939: 284.
Parhyale ochotensis Gurjanova, 1951: 814, fig. 568;—Bulycheva 1957: 82, fig. 28.
Parallorchestes ochotensis Shoemaker 1941: 184 (part);—Bousfield 1981: 75-77, figs.7, 8;—Ishimaru 1994: 69;—Bousfield 2001a: 104.
non: *Parallorchestes ochotensis* Barnard 1962: 160, fig. 23;—Barnard 1979: 119.

Material Examined: Sea of Okhotsk, Dulkert coll., Aug. 5, 1923 - 1 ♂ (22 mm)(slide mount), 1 ♀ ov (22 mm)(slide mount) + 2 ♂♂, 1 ♀, Zool. Mus. No. 5/29540 (Bulycheva det). Japan Sea, Akkeshi, Hokkaido, T. Hiwatari coll, Dec. 23, 1979. - 1 ♂ (21 mm), 1 ♀ ov (21 mm) Coll. Nos. IZ-1983-19.

Diagnosis: Male (to 27 mm). Body large, weakly carinate mid-dorsally on peraeon segments 6 & 7, and moderately strongly on pleon segments 1-3 and urosome segment 1. Antennae relatively long, slender, peduncles well developed. Antenna 1, peduncles posteriorly smooth or nearly so; flagellum 20-22 segmented. Antenna 2, peduncles smooth; flagellum slender, 20-25 segmented.

Mandible, left lacinia 5-dentate; spine row with 2 slender blades. Maxilliped, inner and outer plates apically subtruncate; palp stout, segment 2 distally truncate, dactyl conical, nail short.

Coxal plates 1-3 subquadrate, 2 & 3 with weak hind marginal shelf; coxa 4 broader than deep. Coxa 5 medium deep, aequilobate. Coxa 6 shallowly posterolobate, anterior lobe small. Coxal gills large, broadly heart-shaped, L-shaped and largest posteriorly.

Gnathopod 1 medium; hydrodynamic lobe on basis and ischium small; carpal lobe relatively narrow, margin with 6-8 comb setae; propod subrectangular, slightly broadening distally; dactyl stout, overlapping gently convex, oblique palm. Gnathopod 2, basis with medium hydrodynamic lobe; carpal lobe slender,not extending beyond merus; propod subrectangular,palm short, oblique, gently convex; dactyl stout .

Peraeopods 3 & 4 medium slender; segment 6 with 2-3 weak posterior marginal and distal clasping spines; dactyls medium strong, inner marginal seta minute. Peraeopods 5-7 medium, bases slightly heteropodous, hind margins very weakly crenulated, each with small notch and surge seta; anterior margins with medium spines. Peraeopod 5, segment 4 slightly broadened; segment 5 short, subequal to 1/2 segment 6. Peraeopods 6 & 7, segment 4 little broadened, subequal in length to segment 6.

Epimeral plates 2 & 3, hind corners slightly acuminate, lower margins bare. Uropod 1, peduncle slightly shorter than rami, margins with 5-6 spines and short

Key to North American Pacific Species of *Parallorchestes* Shoemaker

1. Body large (14-30 mm at maturity); posterior peraeon and abdominal segments mid-dorsally carinated (except *P. cowani*); antennae elongate A2 flagellum 15+ segments. . . . . 2.
   Body small to medium (7-13 mm); posterior peraeon and abdominal segments not (or faintly) carinated; antenna short A2 flagellum < 12 segments . . . . . 6.

2. Peraeon segments 6 & 7 variously carinated. . . . . 3.
   Peraeon segments 6 & 7 not carinated . . . . . 4.

3. Peraeon segment 1-5 not carinated; posterior carinations acute; peraeopods 5-7 slender, segment 6 with weak anterior marginal spines . . . . . *P. ochotensis* (Brandt) (p. 37)
   Peraeon segment 1-4 conspicuously carinated; posterior carinations rounded; peraeopods 5-7 short, stout, anterior marginal (clasping) spines strong . . . . . ***P. carinata*** n. sp. (p. 40)

4. Abdominal carinations low, distinct; uropod 1, outer ramus multispinose; mandibular left lacinia 6-dentate . 5.
   Abdominal carinations indistinct; uropod 1, outer ramus with 5-6 marginal spines; mandibular left lacinia 5-dentate. . . . . ***P. cowani*** n. sp. (p. 44)

5. Antenna 1, peduncular segment 1 with 2-3 short posterior marginal spines; peraeopod 5, basis longer than wide; segment 4 short, wide . . . . . ***P. subcarinata*** , n. sp. (p. 41)
   Antenna 1, peduncular segment 1 with 0-1 posterior marginal spines; peraeopod 5, basis broad, wider than long; segment 4 regular, longer than wide . . . . . ***P. alaskensis*** n. sp. (p. 42)

6. Body segments each conspicuously ridged or ribbed at posterior margin; peraeopod 5, segment 5 short, wider than long; animals small (7-10 mm) . . . . . 7.
   Body segments not or inconspicuously ribbed at posterior margin; peraeopod 5, segment 4 regular, longer than wide; animals medium-sized (11-14 mm) . . . . . 8.

7. Antenna 1, peduncular segment 2 very short, little longer than segment 3; antenna 1, segments nearly bare; uropod 3, outer ramus with m arginal spine group . . . . . *P. americana* Bousfield (p. 58)
   Antenna 1, peduncular segment 2 distinctly longer than segment 3; antenna 1, segments of peduncle and flagellum setose posteriorly; uropod 3, ramus lacking margin spines. . . . . *P. asiatica* Tzvetkova (p. 54)

8. Peraeopods 5-7, segment 6 with 3 stout anterior marginal clasping spines; uropod 3, outer ramus long, with 3 groups of marginal spines . . . . . ***P. trispinosa*** n. sp. (p. 60)
   Peraeopods 5-7, segment 6 anterior margin with weak spines or 2 groups of stout spines; uropod 3, ramus subequal to peduncle, with 0-2 groups of marginal spines . . . . . 9.

9. Antenna 1 peduncle & flagellum, posterior margins conspicuously setose; peraeopods 5-7 anterior margin of segment 6 with 2 stout clasping spines . . . . . 10.
   Antenna 1, posterior margins of segments bare or slightly setose; peraeopods 5-7, anterior margin of segment 6 with 3 (or more) weak spines . . . . . 11.

10. Uropod 1, outer ramus with 4 marginal spines; uropod 3, outer ramus margin bare. . . . . *P. zibellina* (Derzhin) (p. 52)
    Uropod 1, outer ramus with 1-2 marginal spines; uropod 3, outer ramus with 1-2 marginal spines . . . . . ***P. kabatai*** n. sp. (p. 53)

11. Antenna1 distinctly shorter than antenna 2; uropod 1, outer ramus with 5-6 marginal spines. . . . . ***P. leblondi*** n. sp. (p. 48)
    Antenna 1, length subequal to antenna 2; uropod 1, outer ramus with 3 marginal spines . . . . . 12.

13. Antenna 1, peduncular setae strong; mature animals small (7 mm) . . . . . ***P. minima*** n. sp. (p. 49)
    Antenna 1, peduncle bare; animals medium (12-13 mm) . . . . . ***P. nuda*** n. sp. (p. 50)

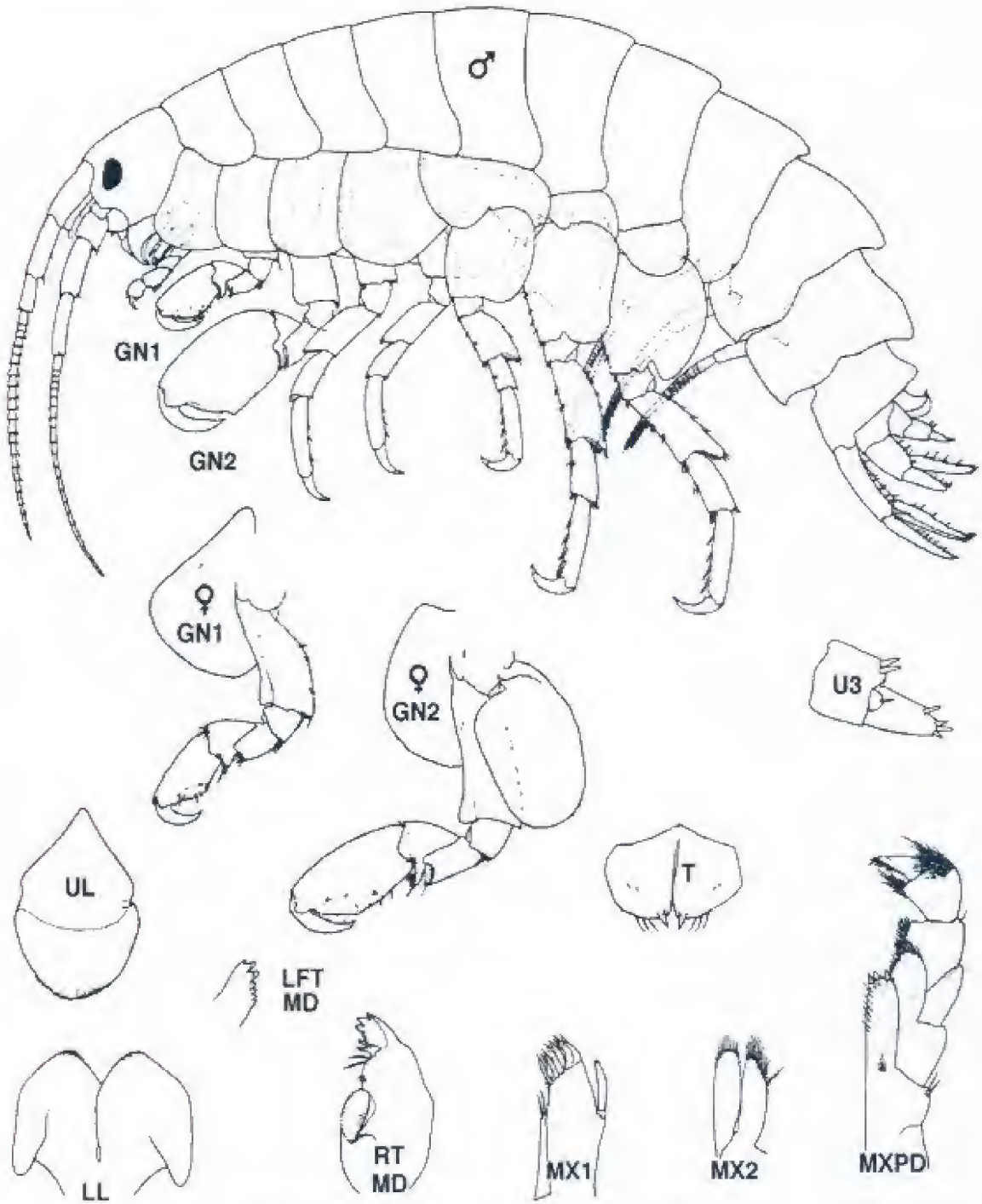

Fig. 16. *Parallorchestes ochotensis* (Brandt, 1851). Male (22 mm); female br. II (22 mm). Okhotsk Sea.

distolateral spine; inner ramus with 3-4 marginal spines; outer ramus with 8-10 closely set marginal spines and short apical spines. Uropod 2, rami each with 3-4 marginal spines, outer ramus distinctly the shorter. Uropod 3 medium,peduncle with 2 posterodistal spines; outer ramus slightly longer than peduncle, with short apical spines and single subapical spine; inner ramus very short, apex with small spine.

Telson lobes short, slightly broader than long, each with single apical spine and 3-4 subapical marginal setae.

Female, br II. (22 mm). Gnathopod 1, basal and ischial lobes very weak; carpal lobe short; propod similar in form but weaker than that of male. Gnathopod 2, basal lobe weak rounded; carpal lobe slender, short; propod subrectangular, broadening distally. Fully developed brood lamellae not described (presumably subovate with rounded apex and long hook-tipped marginal setae). Preamplexing lobe not developed in material available.

Distributional Ecology: Recorded from the Okhotsk Sea and northern Sea of Japan, USSR, and Sakhalin I. Also Dutch Harbour, Alaska, by Holmes (1904), and present material.

Remarks: The naming of this species has undergone a regionally long and checkered history (synonymies above). In North America, J. L. Barnard (1954-1969) has described material from Alaska to southern California under the name *Parallorchestes ochotensis*. However, except for the relatively short antenna 2, his figures and descriptive commentary suggest that the material from Oregon southwards appears mainly referable to *Parallorchestes cowani* n. sp. (p. 44).

The relatively primitive *P. ochotensis* subgroup encompasses *P. subcarinata* and *P. alaskensis* of the Bering Sea region, and the closely related *P. cowani* from SE Alaska to S. California. Component species are typically large, variously carinated,with elongate antennae, weaky crenulated peraeopod bases, and very weakly or undeveloped preamplexing notch in the female.

Parallorchestes carinata n. sp.
(Fig. 17)

Parallorchestes supracarinata Bousfield, 1981: 78 (nomen nudum); Bousfield 2001a: 104.

Material Examined:
Alaska, Aleutians Islands: Amchitka I. (51°29'N, 179°07'W), C.E.O'Clair Stn I A-2, plot 36, Aug. 7, 1972 - ♀ br. II (15.3 mm) **Holotype** (slide mount), CMNC 2002-0083; ♀ br. II (15 mm) **Paratype,** CMNC 2002-0084; Amchitka I., 400 metres south of Kirilof Pt., Constantine Hbr., subtidal algae, P. Slattery coll., Oct. 31, 1971 - 2 ♀♀ subadult.

Bering Sea: St. Paul I., Zolotoi Bay (57° 07'N, 170°17'W) in subtidal agae, P. Slattery coll., June 25, 1983 - 1 ♂ (15 mm) **Allotype** (slide mount), CMNC 2002-0085; 10 ♂♂, 2 ♀♀, 1 juv. **Paratypes,** CMNC 2002-0086.

Diagnosis: Female, br. II. (15.3 mm). Body medium, robust. Peraeon segment 3-7, pleosome segments 1-3, and urosome segment 1 bearing strong, rounded, posterodorsal carinations. Antennae medium long, relatively stout, peduncles well developed. Antenna 1, peduncles 1 & 2 each with small posterior marginal spine cluster; flagellum ~15-segmented. Antenna 2, peduncles 4 & 5 with median clusters of short setae; flagellum slender, 20-22-segmented.

Mandible, left lacinia 5-dentate; spine row with 2-3 slender blades. Maxilliped, inner and outer plates apically rounded; palp medium stout; segment 3 broad; dactyl short, conical.

Coxal plates 1-3 broad, rounded below, lacking hind marginal shelf. Coxa 5 acquilobate. Coxa 6 strongly posterolobate; anterior lobe small, rounded. Coxal gills broadly lobate, slightly largest posteriorly.

Gnathopod 1, basis with small antero-distal lobe; carpal lobe short; propod subrectangular, palm short, shallowly oblique, convex; dactyl closing on paired posterodistal spines. Gnathopod 2, basis and ischium with overlapping hydrodynamic lobes; carpal lobe medium short; propod subrectangular, palm short, very oblique, gently convex, merging with setose posterior margin.

Peraeopods 3 & 4 short, stout; hind margin of segment 6 with 3 striated spines increasing in size distally, and small clasping spine at base of dactyl. Peraeopods 5-7 short, stout; hind margin of basis weakly crenulate, each with notch and surge seta; anterior marginal spines of segment 6 as in posterior marginal spines of peraeopods 3 & 4. Peraeopod 5, segment 4 short, broadest distally; segment 5 shorter than 1/2 segment 6. Peraeopods 6 & 7, segment 4 broadened, shorter than segment 6.

Epimeral plates 2 & 3, hind corners weakly acuminate, lower margins spinulose. Pleopods slender, regular. Uropod 1, peduncle and rami subqual in length, outer margin of peduncle with 6-7 stout spines and medium posterodistal spine; outer ramus tapering distally, with ~10 closely set marginal spines and short apical spine. Uropod 2, outer ramus slightly the shorter, each with 3-4 marginal spines. Uropod 3 short; outer ramus stout, slightly longer than peduncle, with 1-2 clusters of marginal spines, and several short spines lining blunt apex; inner ramus short, apex with minute seta.

Telson lobes evenly broad; apices each with single inner distal spine and 3-4 apical marginal setae.

Preamplexing notch a slight shallow indentation on the anterodistal margin of peraeon 2.

Male (15 mm). Gnathopod 1, hydrodynamic lobe medium on stout, short basis, weak on ischium; carpal lobe weakly setose; propod short, deep, palm oblique; dactyl stout. Gnathopod 2, h.-d. lobe large on basis and ischium; carpal lobe very small, weakly setose; propod large, subquadrate, palm oblique; dactyl regular. Uropod 1, outer ramus with 5 short distal marginal spines. Uropod 3, outer ramus slightly shorter than peduncle.

Etymology: The Latin root name "carinatus" alludes to the strongly keel-shaped ridges of the body.

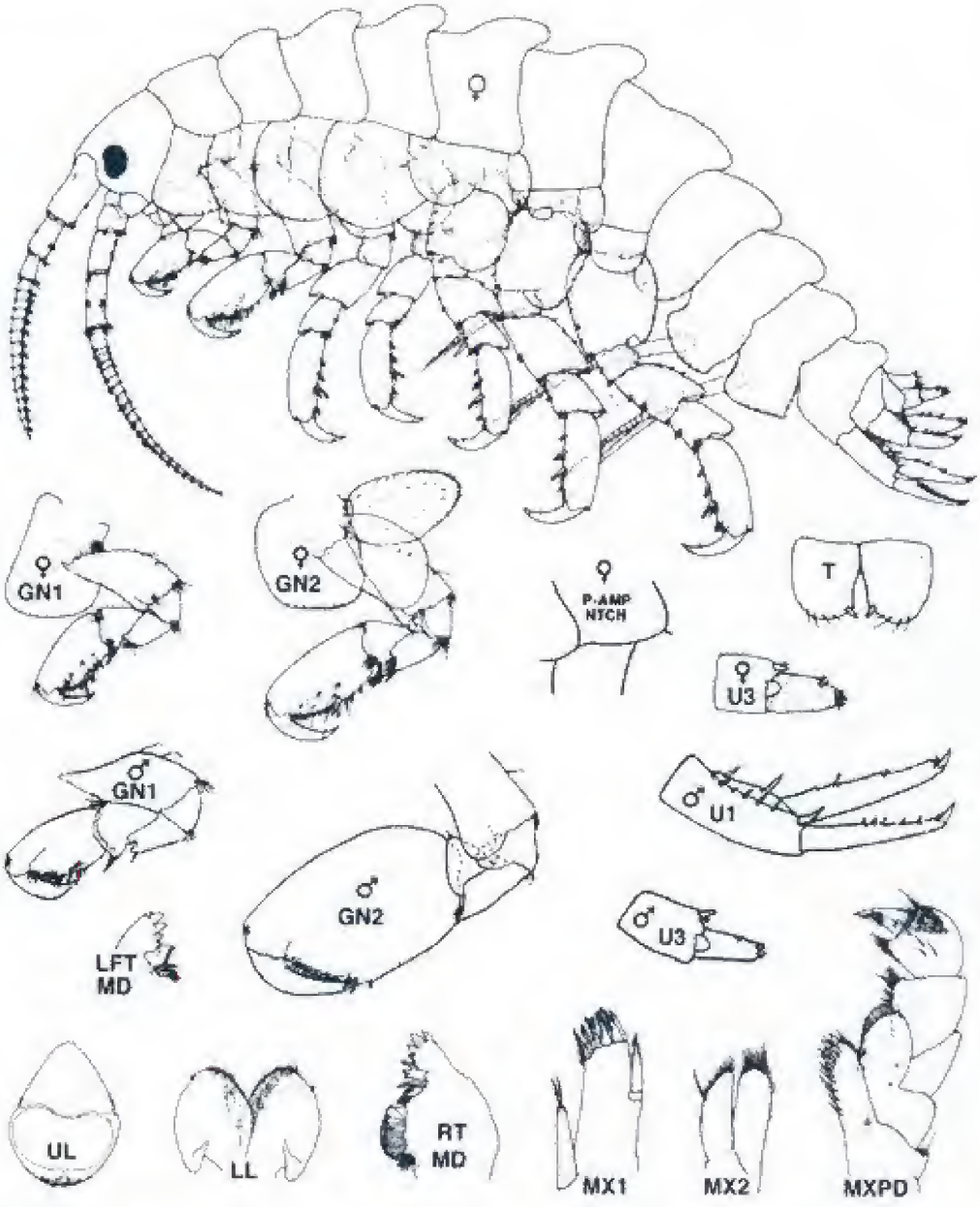

Fig. 17. ***Parallorchestes carinata* n. sp.** Female (br. II) (15.3 mm). Amchitka, Aleutians Islands., Alaska. Male (15.0 mm), Zolotoi Bay, St. Paul I., Bering Sea.

Distributional Ecology: Known only from the type locality, among algae on rocky shores, LW level.

Remarks: In the type specimen of *P. carinata*, the outer ramus of the left uropod 3 bears no marginal spines.

***Parallorchestes subcarinata* n. sp.**
(Fig. 18)

Parallorchestes subcarinata Bousfield, 1981: 78 (nomen nudum); Bousfield 2001a:104.

Material Examined:
Alaska, Aleutian Islands: St. Makarius Bay, Amchitka I., C. E. O'Clair coll. (51° 22' 48"N, 179°13' 30"W), Box 5, 12 m, in *Hedophyllum*, Sept. 20, 1968 - ♂ (16.0 mm) **Holotype** (slide mount), CMNC 2002-0070; ♀ br. II (15.0 mm) **Allotype** (slide mount),CMNC 2002-0053; ♀ br. II (13.3 mm) **Paratype**.

Diagnosis: Male (16.0 mm). Body large and robust. Pleon segments 1-3 and urosome 1 with low mid-dorsal ridge, highest posteriorly. Antennae medium long, stout, peduncles well developed. Antenna 1, peduncle 1with 3-4, and peduncle 2 with single, posterior mar-

ginal spines; flagellum 18-20-segmented. Antenna 2, peduncular segments 4 & 5 with submedian lateral clusters of short spines; flagellum slender, 18-25-segmented.

Mandible, left lacinia 5-dentate; spine row with 3 slender blades. Maxilliped, inner plate subtruncate; outer plates with inner rounded cutting edge; palp medium; segment 3 subtruncate distally; dactyl conical, unguis short.

Coxal plates 1-4 subquadrate, gently rounded below; coxae 2 & 3 with very weak posterior marginal shelf. Coxa 5 shallow, aequilobate. Coxa 6 strongly posterolobate, anterior lobe small, rounded. Coxal gills broadly heart-shaped, largest posteriorly.

Gnathopod 1 medium; basis with weak hydrodynamic lobe; carpal lobe small; propod medium strong, broadening distally, palm distinct, oblique, subequal to hind margin; dactyl simple, slightly overlapping paired posterodistal spines. Gnathopod 2, basis and ischium with overlapping hydrodynamic lobes; carpal lobe thin, shallow; propod subovate, narrowing slightly distally, palm short, oblique, nearly straight; dactyl short.

Peraeopods 3 & 4 relatively slender; segment 6 with 5-6 posterior marginal spines increasing distally, and smaller distal clasping spine; dactyls regular. Peraeopods 5-7 medium stout; bases, hind margins weakly crenulate, each with distinct notch and surge seta; marginal spines of segment 6 as in peraeopods 3 & 4. Peraeopod 5 distinctly shortest; segment 4 slightly broadened. Peraeopod 6, segment 5 slightly longer than 1/2 segment 6. Peraeopods 6 & 7, segment 4 little broadened, subequal in length to segment 6.

Epimeral plates 2 & 3, hind corners very slightly acuminate, lower margins spinulose. Uropod 1, peduncle slightly shorter than rami, margins with 3-5 spines and short posterodistal spine; inner ramus with 3-4 marginal spines; outer ramus with 8-10 closely set marginal spines, and short apical spines. Uropod 2, rami each with 3-4 marginal spines, outer ramus very slightly the shorter. Uropod 3 medium; outer ramus slightly longer than peduncle, with apical spines and 1-2 groups of marginal spines; inner ramus rounded, with small apical spine;

Telson lobes short, broad, each with 2-3 apical spines and 3-4 subapical marginal setae.

Female ov. (15.0 mm): Antenna 2, flagellum less robust and less setose than in male. Gnathopod 1, basis with weak hydrodynamic lobe; carpal lobe small; propod relatively slender, palm shorter than posterior margin. Gnathopod 2 subsimilar but propod larger and slightly broadening distally. Brood lamellae not mature. Preamplexing notch not distinct.

Etymology: From the Latin root names "sub" and "carinatus", with reference to the low mid-dorsal carinations on the abdominal segments.

Distributional Ecology: Low intertidal, Aleutian Islands (Amchitka I.) south to Kruzof I, Southeastern Alaska.

Parallorchestes alaskensis n. sp.

(Fig. 19)

Parallorchestes crenulata Bousfield, 1981: 78 (nomen nudum)

Material Examined:

Alaska, Aleutian Islands: Massacre Bay, Attu I., LW level, C. E. O'Clair coll., June 23, 1972 - ♀ (br. II) (16.0 mm) **Holotype** (slide mount), CMNC 1983-1512; ♀ (br. II) **Paratype**, CMNC 1983-1513.

Diagnosis: Female, br. II (16.0 mm). Body medium large, robust. Peraeon segments 6 & 7 and pleosome segments 1-3 each with low rounded posterodorsal carination. Eyes relatively large, short-ovate. Antennae medium long, slender, peduncles well developed. Antenna 1, peduncular segments 1 & 2 each with single posterior mid-marginal spine; flagellum 17-18-segmented. Antenna 2, peduncles 4 & 5 with short median posterior spine; flagellum slender, 20-22-segmented.

Mandible, left lacinia 6-dentate; spine row with 2 unequal slender blades. Maxilliped, inner plate apically subtruncate, outer plate distomedially squared.

Coxal plates 1-3 gently rounded, lacking hind marginal cusps; coxa distinctly rounded below. Coxa 5 posterolobate.

Gnathopod 1 medium slender; propod slender, length twice depth, palm distinct, oblique; dactyl tip closing on paired posterodistal spines. Gnathopod 2 similar but larger; basis with distinct hydrodynamic lobe; propod subrectangular, narrowing slightly, palm distinct, oblique, nearly straight; carpal lobe medium, longer and narrower than in gnathopod 1.

Peraeopods 3 & 4 medium; segment 6 distinctly longest, clasping spine weak to medium; dactyls slender. Peraeopods 5-7 medium stout, bases with variously rounded weakly crenulate hind margins; clasping spines of segment 6 medium. Peraeopod 5, segment 4 short, broad; segment 5 about equal to 1/2 segment 6. Peraeopods 6 & 7, segment 4 somewhat broadened, shorter than segment 6.

Epimeral plates 2 & 3, hind corners nearly squared, lower margins nearly bare. Uropod 1, peduncle subequal in length to rami, margins with 4-6 stout spines and

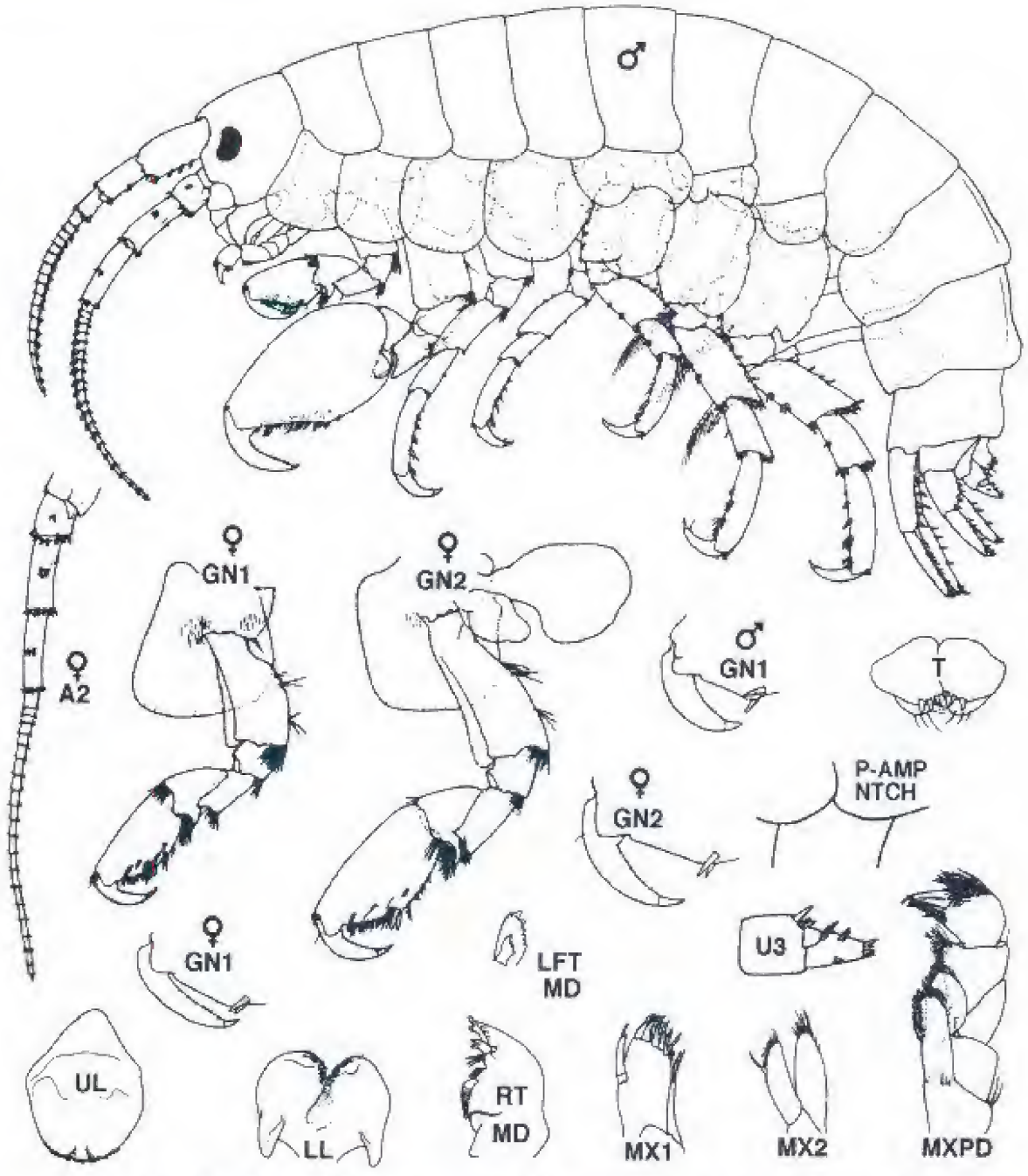

Fig. 18. ***Parallorchestes subcarinata* n. sp.** Male (16 mm); female br. II (15 mm).

in length to rami, margins with 4-6 stout spines and short posterodistal spine; rami slightly tapering, subequal, outer ramus with ~10 closely set marginal spines and short apical spine. Uropod 2, rami each with 4-5 marginal spines, outer ramus slightly the shorter. Uropod 3, inner ramus short, bare (?); outer ramus not longer than peduncle, with short apical spines and marginal spines.

Telson lobes broad, each with single apical spine and 3-5 subapical marginal setae.

Brood plates in developmental stage II; preamplexing notch not distinct in female specimens examined.

Male unknown.

Etymology: The name alludes to the species type locality in the Aleutian island chain of Alaska.

Distributional Ecology. Rocky shores, among algae, LW level. Known only from the type locality, Attu I., Aleutian Islands, Alaska.

Remarks: *Parallorchestes alaskensis* is a member of the *ochotensis* group of large, stout-bodied posteriorly carinated species. This species is distinguished by its low rounded posterior carinations, short broad segment 4 of peraeopod 5, slender peraeopod dactyls, and short outer ramus of uropod 3.

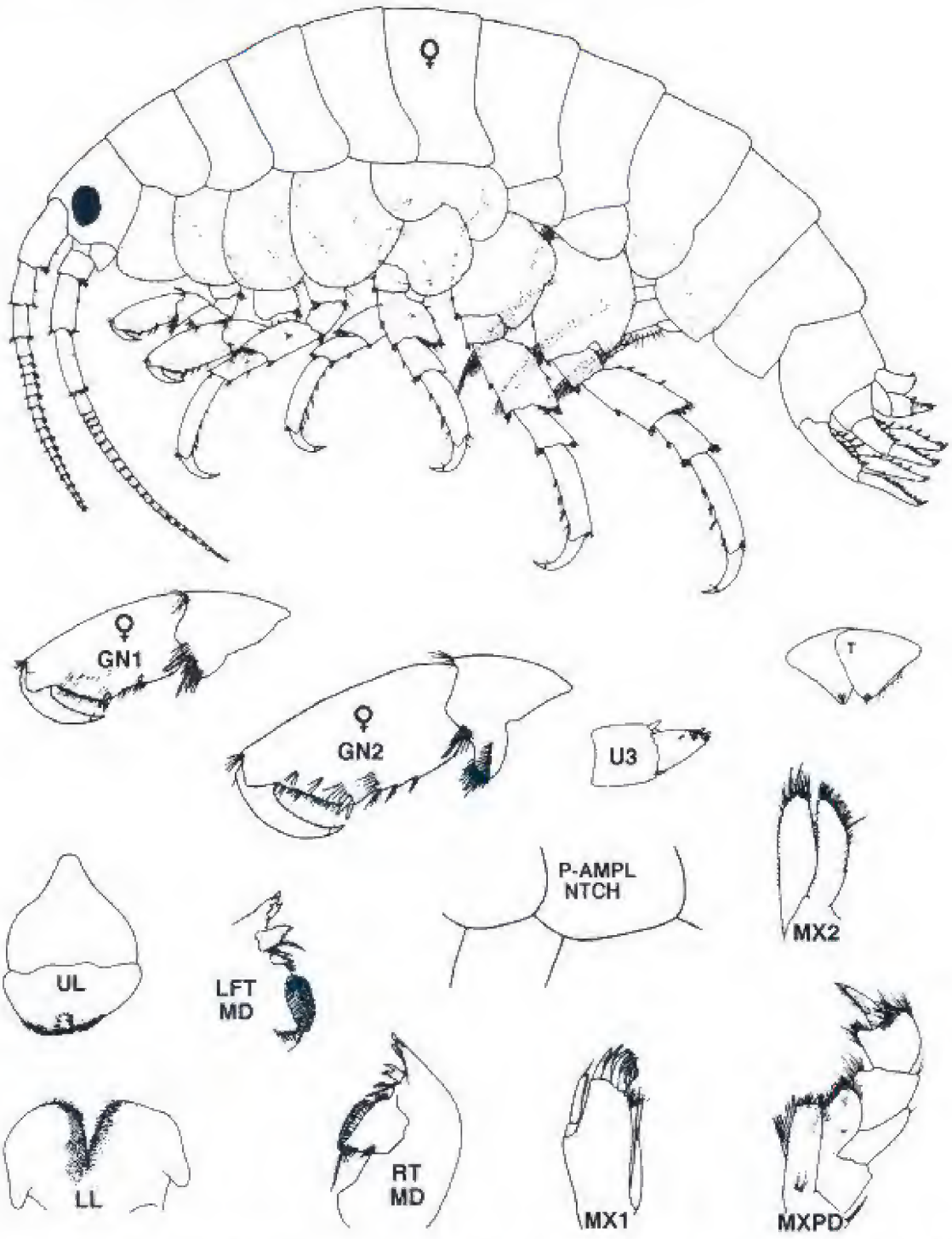

Fig. 19. ***Parallorchestes alaskensis* n. sp.** Female (br II) (16.0 mm) Attu I., Aleutians Ids., Alaska.

***Parallorchestes cowani* n. sp.**
(Fig. 20)

Parallorchestes ochotensis Barnard 1952: 23, pl. 5, fig. 1;—Barnard 1954: 24 (Cape Arago, ORE);—Barnard 1964: 118;—Barnard 1969b: 141 (Carmel);—Barnard & Karaman 1991: 371 (part).

Parallorchestes spinosa Bousfield, 1981: 78 (nomen nudum;—Bousfield 2001a: 104.

Material Examined: ~970 specimens in 110 lots, SE Alaska to central California. ELB Station references: Bousfield (1958, 1963, 1968); Bousfield & McAllister (1962); Bousfield & Jarrett (1981).

ALASKA

Aleutian Islands: Plot #1, Cyril Cove, Amchitka I., C. E. O'Clair coll., 1969 - 1 ♂, 1 ♀; (2 lots). Stn. IA-2, Amchitka I., C. E. O'Clair coll., 1972 - 1974- 1 ♂; (6 lots)

Southeastern Alaska: ELB Stns, 1961: A3 (2), A6 (1), A7 (few), A18 (6), A19 (82), A22 (88), A23 (61), A25 (6), A42

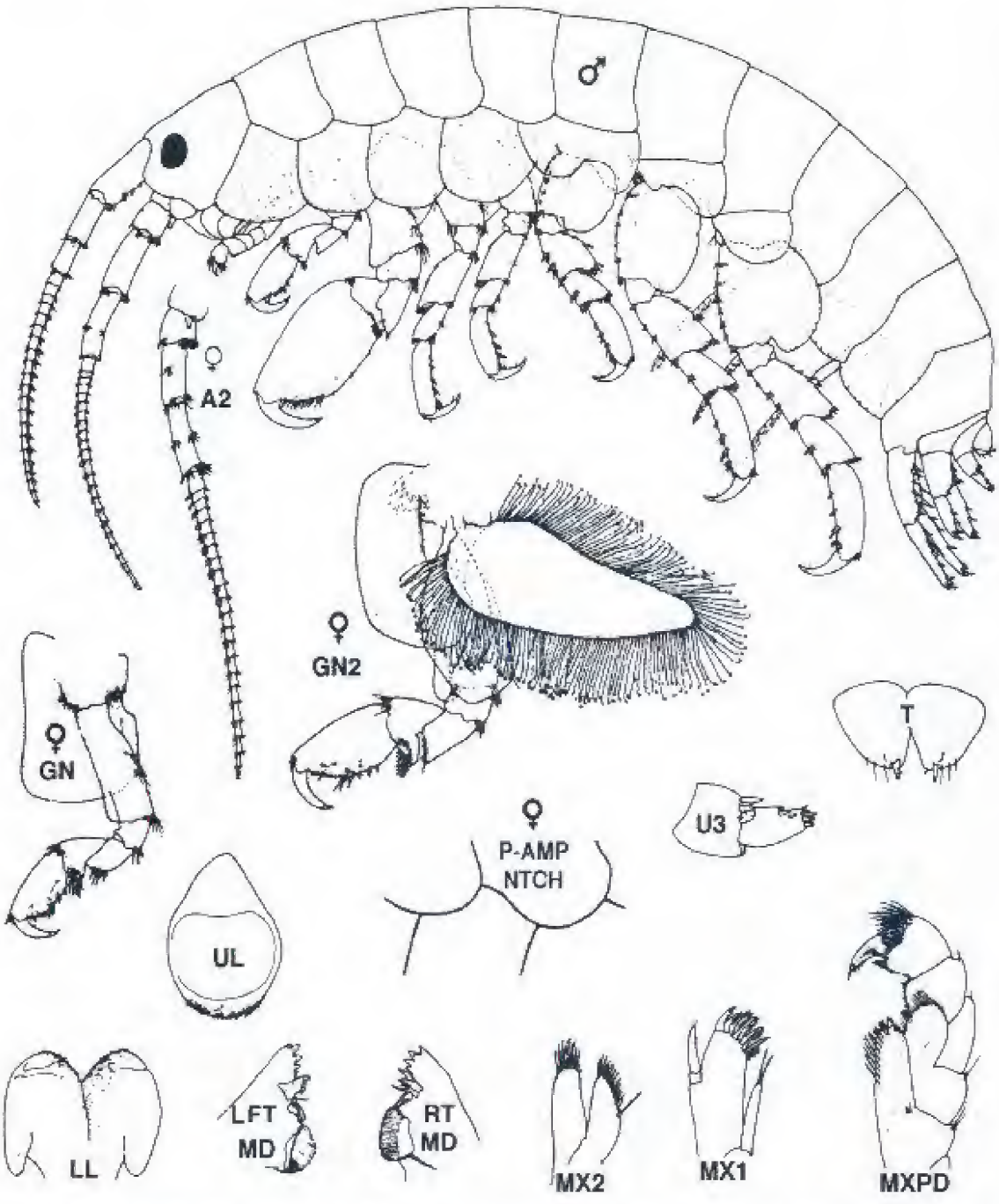

Fig. 20. ***Parallorchestes cowani* n. sp.** Male (13.0 mm); female ov (14.0 mm). Brady Beach, V. I.

(2), A48 (13), A57 (21), A71 (4), A75 (61), A80 (16), A121 (4), A147 (33), A159 (1), A164 (67) A168 (1), A171 (3), A175 (1) A177 (1).
ELB Stns, 1980: S20B6 (1 ♂, photo'd), S18B1 (1 ♂, 1 ♀).

BRITISH COLUMBIA
Queen Charlotte Islands: ELB Stns, 1957: E14a (17), E21 (9), E25 (3); H2 (13); W1 (4), W2 (14), W4 (20), W8 (17), W11 (17), W12 (5), W14a (6), W14b (1), W17 (1).
North Central Coast: ELB Stns, 1964: H1 (15), H7 (4), H10 (43), H16 (7), H23 (2), H29 (6). H32 (2), H33 (27), H35 (75), H39 (96), H48 (1), H57 (10), H65 (3).
South Central coast: ELB Stn, 1955: M2 (3).
Northern Vancouver Island: ELB Stns, 1959: N1 (1), N5 (7), N6 (31), N16 (30); O1 (3), O11 (1), O13 (1), O15 (1); V4b (7), V11 (9), V18 (6).
Southern Vancouver Island: ELB Stns, 1955: F1 (12), F2a (7), F3 (3), F4 (3), F5 (3), F5b (4); G2 (5), G11 (8); P4 (7), P7 (3).
ELB Stns, 1964: H40 (51), H43 (14), H44 (180).
ELB Stns, 1970: P703 (54), P711 (5), P715 (16), P716 (19), P719 (28), P21 (11).
ELB Stns, 1975: P3b (1), P20a (529 males, females), P20b (73), P21a(1)B28 (5).

ELB Stns, 1976: B3 (26), B5 (75), B12b (3), B13 (32).
ELB Stns, 1977: B12e (1) Brady Beach, V. I..(48°49'08"N, 125°08'03"W) - ♂ (13.0 mm) **Holotype** (slide mount), CMNC 2002-0054; ♀ov (14.0 mm) **Allotype** (slide mount), CMNC 2002-0078.
Additional British Columbia material: J. F. L. Hart Stns: Brentwood Bay, 1928 - 1 ♀; Gonzales Bay, 1934 - 1 ♀.
R. K. Lee Stns: Glacier Pt., 1969 - 6♂♂, 7♀♀, 2 im; Botany Beach, 1971 - 16 im; Whiffen spit, 1973 -1 ♀.
D. Kittle Stns: No. 36, S. Pender I. - 10 im; No. 59B, Anguilar Pt. - 2 im; No. 337, Cable Beach - 2 im; No. 757, Small I., 1972 - 4 im.
C. L. Lobban Stns, 1971: CL-1011, Rocky Pt., Wickaninnish Bay - 1 im; CL-1032, Broken Group - 11 ♀♀, 7 ♂♂, 30 im.

WASHINGTON -OREGON
ELB Stns, July-Aug., 1966: W5 (6), W30 (319), W34 (9), W35 (26), W36 (60), W57 (24), W60 (86). Eagle Cove, San Juan I., R. M. O'Clair Stn 74001, 1974 - 8 ♂♂, 9 ♀♀.

Diagnosis: Male (to 14.0 mm). Body medium large, robust. Peraeon, pleon and urosome segment 1 segments dorsally smooth or posteriorly with very low mid-dorsal ridge. Antennae medium long, slender, peduncles strong. Antenna 1, peduncle 1 with small posterior marginal spines; flagellum ~20-segmented. Antenna 2, peduncular segments 4 and 5 with a few mediolateral clusters of short spines and setae and posteromedial setal cluster; flagellum slender, nearly bare, ~25 segmented.

Mandible, left lacinia 5-dentate; spine row with 2 slender blades. Maxilliped, inner and outer plates apically rounded; palp medium; segment 3 broad; dactyl relatively long, curved

Coxal plates 1-3 subrectangular, slightly convex below, 2 & 3 with slight hind marginal shelf. Coxa 5 aequilobate. Coxa 6 strongly posterolobate, anterior lobe small. Coxal gills broadly lobate, subequal in size and form.

Gnathopod 1 small; basis with weak hydrodynamic lobe; carpal lobe small; propod slender, slightly broadening distally, palm short, oblique; dactyl simple, slightly over-lapping paired posterodistal spines. Gnathopod 2, basis and ischium with sharply rounded and overlapping hydrodynamic lobes; carpal lobe narrow, short; propod subrectangular, narrowing slightly distally, palm short, oblique, gently convex.

Peraeopods 3 & 4 medium stout; segment 4 short; segment 6 with 4-5 posterior marginal spines, enlarging distally; dactyls relatively slender. Peraeopods 5-7 medium stout; bases, hind margins weakly crenulate, each with distinct notch and surge seta; segment 6 with 3-4 medium strong anterior marginal spines. Peraeopod 5, segment 4 slightly broadened distally; segment 5 short, slightly longer than 1/2 segment 6. Peraeopods 6 & 7, segment 4 little broadened, subequal in length to segment 6.

Epimeral plates 2 & 3, hind corners slightly acuminate, lower margins sparsely spinulose. Uropod 1, peduncle slightly shorter than rami, outer margin with 4-5 spines and short (<1/3 ramus) posterodistal spine; rami with 3-4 marginal spines and short apical spines. Uropod 2, outer ramus slightly the shorter, each with 2 marginal spines. Uropod 3 medium short; outer ramus slightly longer than peduncle, with short apical spines and 1-2 clusters of posterior marginal spines; inner ramus small, with minute apical seta.

Telson lobes tapering to blunt apex, each with single apical spine and 3-4 subapical marginal setae.

Female ov. (14.0 mm). Antenna 2, peduncular segments 4 & 5 slightly more spinose-setose than in male. Gnathopod 1 similar to, but slightly smaller than that of male; basis virtually lacking anterodistal lobe. Gnathopod 2, basis and ischium with prominent anterodistal lobes; carpal lobe full; propod broader and larger than in gnathopod 1, lower margin with distal setal clusters. Brood plate (gnathopod 2) relatively narrow, elongate, tapering and sharply rounded distally, with 50-60 long, numerous curl-tipped marginal setae on each side. Preamplexing notch a shallow indentation on the anterodistal margin of peraeon segment 2.

Etymology: The patronym recognizes the outstanding career contributions of Dr. Ian McTaggart-Cowan, former Dean of Science, University of British Columbia, in the development, teaching, and dissemination of knowledge of the Canadian coastal marine fauna.

Distributional Ecology: From the Aleutian Islands, southeastern Alaska, and British Columbia, south through Washington and Oregon to central California, sporadically south to Laguna Beach; free-swimming or clinging to brown algae & *Phyllospadix* at LW level, along exposed and semi-protected rocky shores.

Remarks: *Parallorchestes cowani* is the most frequently encountered species on the North American Pacific coast, previously referred to by other N. American authors as "*P. ochotensis*". Illustrations and descriptions of J. L. Barnard (1952, 1954, 1969b), pertaining to both mature and immature specimens from Oregon and central California, appear referable to this species. However, the unillustrated material recorded from Bahia de St. Quentin , Baja California, by Barnard (1964) is here considered problematical.

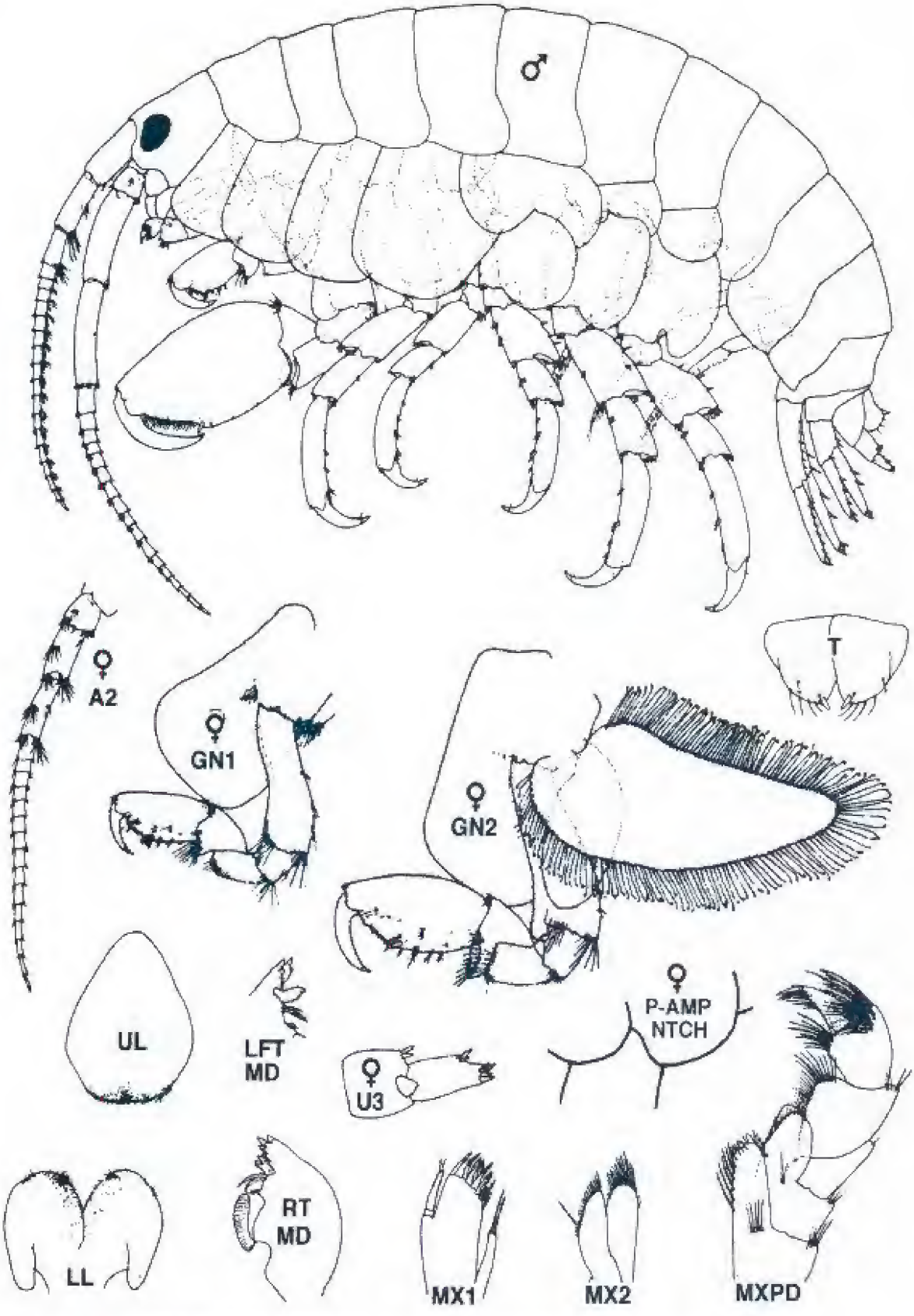

Fig. 21. ***Parallorchestes leblondi*** n. sp. Male (11.0 mm); female ov (11.0 mm).
ELB Stn. P715, Gonzales Bay, Victoria, B. C.

Parallorchestes leblondi n. sp.
(Fig. 21)

Parallorchestes brevicornis Bousfield 1981: 77 (nomen nudum); —Bousfield 2001a: 104 .

Material examined: ~150 specimens in 14 lots, Southern British Columbia to Oregon. ELB Station references: Bousfield (1958, 1963, 1968), Bousfield & McAllister (1962); Bousfield & Jarrett (1981).

BRITISH COLUMBIA

Southern Vancouver I.: 1955, ELB Stn: P6a, Wickaninnish Bay at Moraes Beach, sand near rocks, LW level - 1 ♂ (slide mount); 4 ♂♂, 4 ♀♀.
1959, ELB Stn: O17, Midway Rocks, Wickaninnish Bay, exposed MW rock pools - 4 im.
1970, ELB Stns: P707, Pachena Bay (48° 47.5' N, 125° 07' W), surf exposed sand, boulder, *Phyllospadix* at LW, July 16 (4 lots) - 17 ♂♂, 17 ♀♀ov, 20 im; P715, Gonzales Bay, Victoria (48° 25'N, 123° 20'W), among algae on fine sand over pebbles at LW, July 29 - ♂ **Holotype** (11.0 mm) (slide mount), CMNC 2002-0055; ♀ ov (11.0 mm) **Allotype** (slide mount), CMNC 2002-0056.
1976, ELB Stns: B3 (1), B6 (1); B12 (2 lots) - 14 ♂♂, 15 ♀♀, 13 im; 1977, ELB Stns. B4a (1); B19b (1 im).

WASH.-OREGON

1966, ELB Stns: W22 (1); W24 (3 lots)(2 males, 5 females, 2 im); W50 (9); W53 (8); W57 (2).

Diagnosis: Male (11.0 mm). Body dorsally smooth or nearly so. Peraeon segments with slight posterior marginal thickening. Antennae relatively long, slender, peduncles very well developed. Antenna 1, peduncular segments 1 & 2 with small posterior marginal spines; 2 & 3 with posterodistal clusters of setae; flagellum of about 20 posteriorly weakly setose segments. Antenna 2, peduncular segments 4 & 5 nearly bare; flagellum slender, 17-18 segmented.

Mandible, left lacinia 5-dentate; spine row with 2 slender blades. Maxilliped, inner and outer plates apically rounded; palp medium stout; dactyl strong, unguis relatively long.

Coxal plates 1-3 large, deep rectangular, each with blunt hind marginal shelf. Coxa 5 aequilobate. Coxa 6 strongly posterolobate, anterior lobe small. Coxal gills large, broadly lobate, slightly largest on peraeopod 6.

Gnathopod 1 medium; basis with small hydrodynamic lobe; carpal lobe short; propod short-rectangular, lower margin distally with short setae, palm short, oblique; dactyl simple, stout, distinctly overlapping paired posterodistal spines. Gnathopod 2, basis and ischium with strong overlapping hydrodynamic lobes; carpal lobe very slender; propod subrectangular, narrowing slightly distally, palm short, oblique, nearly straight.

Peraeopods 3 & 4 medium stout; segment 6 with relatively weak posterior marginal spines; dactyls regular. Peraeopods 5-7 medium stout; bases, hind margins weakly crenulate, each with distinct notch and surge seta; clasping spines of segment 6 medium strong. Peraeopod 5, segment 4 slightly broadened; segment 5 slightly longer than 1/2 segment 6. Peraeopods 6 & 7, segment 4 little broadened, slightly shorter than segment 6.

Epimeral plates 2 &3, hind corners slightly acuminate. Uropod 1, peduncle slightly shorter than rami, margins with 3-4 spines and short distolateral spine; inner ramus with 2 marginal spines, outer ramus with 6-7 shorter, close-set marginal spines and 2-3 short apical spines. Uropod 2, outer ramus slightly the shorter, each with 2 marginal spines. Uropod 3 medium; outer ramus slightly longer than peduncle, with apical spines and 1-2 clusters of posterior marginal spines.

Telson lobes short, broadly rounding to obtuse apex; with single apical spine and 4 subapical marginal setae.

Female ov. (11.0 mm). Antenna 2, peduncular segments facially and marginally more setose than in male. Gnathopod 1 similar to that of male, but dactyl more slender. Gnathopod 2, bais and ischium with distinct hydrodynamic lobes; carpal lobe small; propod larger and deeper than in gnathopod 1. Brood plate (gnathopod 2) basally broad, tapering and sharply rounded distally, marginal setae relatively short. Preamplexing notch shallow; posterior distal lobe deep, width ~4/5 that of peraeon 2.

Etymology: The species is named in honour of Dr. Paul H. LeBlond, retired Professor of Oceanography, University of British Columbia, for his leadership in the research and teaching of ocean sciences.

Distributional ecology: Exposed sandy and rock beaches, at LW level, from central west coast of Vancouver I., B. C., south to Oregon.

Remarks: *Parallorchestes leblondi* exhibits an unique combination of character states that, in balance, is intermediate between those of the primitive *ochotensis* group and the more advanced *zibellina* group (p. 52).

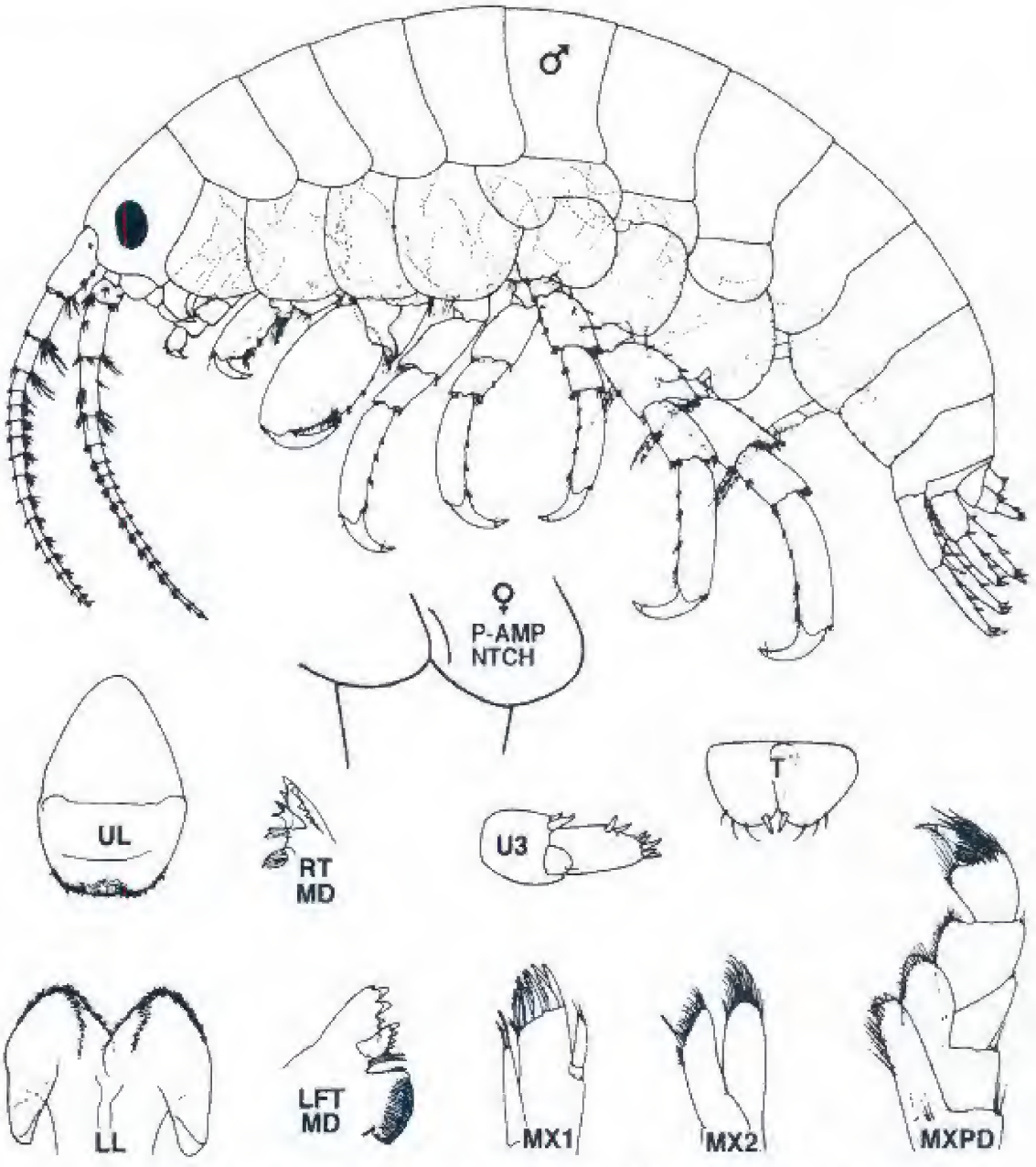

Fig. 22. ***Parallorchestes minima* n. sp.** Male (7.0 mm); female (4.5 mm). Stn. V4, Roller Bay, Vancouver I., B. C..

***Parallorchestes minima* n. sp.**
(Fig. 22)

Parallorchestes minima Bousfield, 1981: 78 (nomen nudum); — Bousfield 2001a: 104.

Material Examined:
BRITISH COLUMBIA
Northern Vancouver I.: ELB Stn, 1959: V4b, Roller Bay, Hope I. (50° 5'N, 127° 56'W), among *Phyllospadix* and brown algae, over boulders and coarse sand, LW, July 22 - ♂ (7.0 mm) **Holotype** (slide mount), CMNC 2002-0057; ♀ ov (4.5 mm) **Allotype** (slide mount), CMNC 2002-0058 ; 1 im **Paratype.**

Diagnosis: Male (7.0 mm). Body smooth, segments lacking posterior ridges or carination. Eye broadly ovate. Antennae and peduncles medium strong. Antenna 1, peduncular segments 1-3 each with posterodistal cluster of setae; segment 1 with 2 small posterior marginal spine groups; flagellum ~14-segmented, segments with small posterodistal setal clusters. Antenna 2, peduncular segments 4 & 5 relatively short, extending little beyond peduncle of antenna 1, each with middorsolateral and posterodistal setal clusters; flagellum 12-14-segmented.

Mandible: lacinia 5-segmented; spine row with 2 slender blades. Maxilliped, inner plate apically

subtruncate; outer plate with sharply rounded inner distal cutting edge; palp segment 2 broad, distally truncate; segment 3 slender; dactyl strong, unguis distinct.

Coxae 2-3 large, broad, with distinct rounded hind marginal cusps, lower margins near straight. Coxa 5 aequilobate. Coxa 6, strongly posterolobate, anterior lobe small, shallowly rounded below. Coxal gills medium, relatively slender, especially on peraeopod 6.

Gnathopod 1 medium; basis and ischium with distinct overlapping hydrodynamic lobes; carpal lobe setose; propod slender, subrectangular, palm short, oblique; dactyl simple, slightly overlapping paired postero-distal spines. Gnathopod 2, basis and ischium with strong hydrodynamic lobes; carpal lobe relatively thick; propod subovate, palm short, very oblique, nearly straight; dactyl regular.

Peraepods 3 & 4 medium stout; segment 6 with 3 short posterior marginal spines. Peraeopods 5-7 medium stout, bases very broad, hind margins crenulate, dactyls medium. Peraeopod 5, segment 4 not broader than long, little longer than segment 5, and about 1/2 length of segment 6. Peraeopods 6 & 7, segment 4 slightly broadened, longer than 1/2 segment 6, clasping spines very weak.

Epimeral plates 2 & 3, hind corners very slightly acuminate, lower and hind margins weakly spinose. Uropod 1, peduncle shorter than rami, outer margin with 3-4 short spines and medium strong distolateral spine; rami with 2-3 marginal spines and short apical spines. Uropod 2, outer rami distinctly shorter than inner ramus, each with 2 marginal spines. Uropod 3 medium, outer ramus longer than peduncle, with apical and single posteromarginal clusters of medium spines; inner ramus small, with small subapical seta.

Telson lobes short, apex rounded, each with single apical spines and 3 short subapical marginal setae.

Female ov (6.5 mm). Gnathopod 1 similar to that of male. Gnathopod similar to male, but propod smaller. Brood plates large broad, tapering distally, marginal setae very long. Preamplexing notch indiscernible; small lunate depression on surface of peraeon 2, near hind border with peraeon segment 1.

Etymology: From the Latin "minimus" - least with reference to the small size of the adult stage.

Distributional Ecology: Known only from the type locality on NorthVancouver I., B. C., among *Phyllospadix* and kelp, over bedrock and boulders, LW level.

Remarks: The species is similar to *P. nuda* but differs in having the antennae subequal in length, and outer ramus of uropod 1 with 3 marginal spines only.

Parallorchestes nuda n. sp.
(Fig. 23)

Parallorchestes nuda Bousfield, 1981: 78 (nomen nudum) ;—Bousfield 2001a: 104.

Material Examined:
BRITISH COLUMBIA
Southern Vancouver I.: ELB Stn P6a, Moraes Beach, Wickaninnish Bay, sand at LW level, Aug. 2, 1955 - ♂ (12.0 mm) **Allotype** (slide mount) CMNC 2002-0060; ♀ ov (13.0 mm) **Holotype** (slide mount), CMNC 2002-0059. Ogden Pt., Victoria, coll. J.F.L.Hart & G. C. Carl, July 18, 1955 - ♂ (7.0 mm).

Diagnosis: Female ov. (13.0 mm). Body smooth, segments lacking posterior ridges. Antennae and peduncles medium short. Antenna 1, peduncular segments 1-3 each with posterodistal cluster of short setae; segment 2 with small posteromarginal spine group; flagellum ~20-segmented, segments with small posterodistal setal clusters. Antenna 2, peduncular segments 4 shorter than 5, each with mid-dorsolateral setal cluster; flagellum ~15-segmented.

Mandible: lacinia 5-segmented; spine row with 2 unequal slender blades. Maxilliped, inner plate apically subtruncate; outer plate with squarish inner distal cutting edge; palp segment 2 broad, deep, distally subtruncate; dactyl curved, longer than segment 3.

Coxae 2-3 large, broad, with weak hind marginal shelf, lower margins nearly straight. Coxa 5 distinctly anterolobate. Coxa 6, shallowly posterolobate, anterior lobe small, shallowly rounded below. Coxal gills medium, relatively slender, especially on peraeopod 6.

Gnathopod 1 medium; basis with medium strong hydrodynamic lobe; ; propod slender, subrectangular, hind margin with 1-2 setal groups, palm short, oblique; dactyl simple, slightly overlapping paired posterodistal spines. Gnathopod 2, hydrodynamic lobes of basis and ischium very weak or lacking; carpal lobe medium; propod subrectangular, much stronger than in gnathopod 1; palm short, oblique; dactyl regular.

Peraeopods 3 & 4 medium stout; segment 6 with short posterior marginal spines; dactyls medium. Peraeopods 5-7 medium stout; bases very broad, hind margins crenulate,each with weak notch and surge seta; dactyls medium. Peraeopod 5, segment 4 broad-

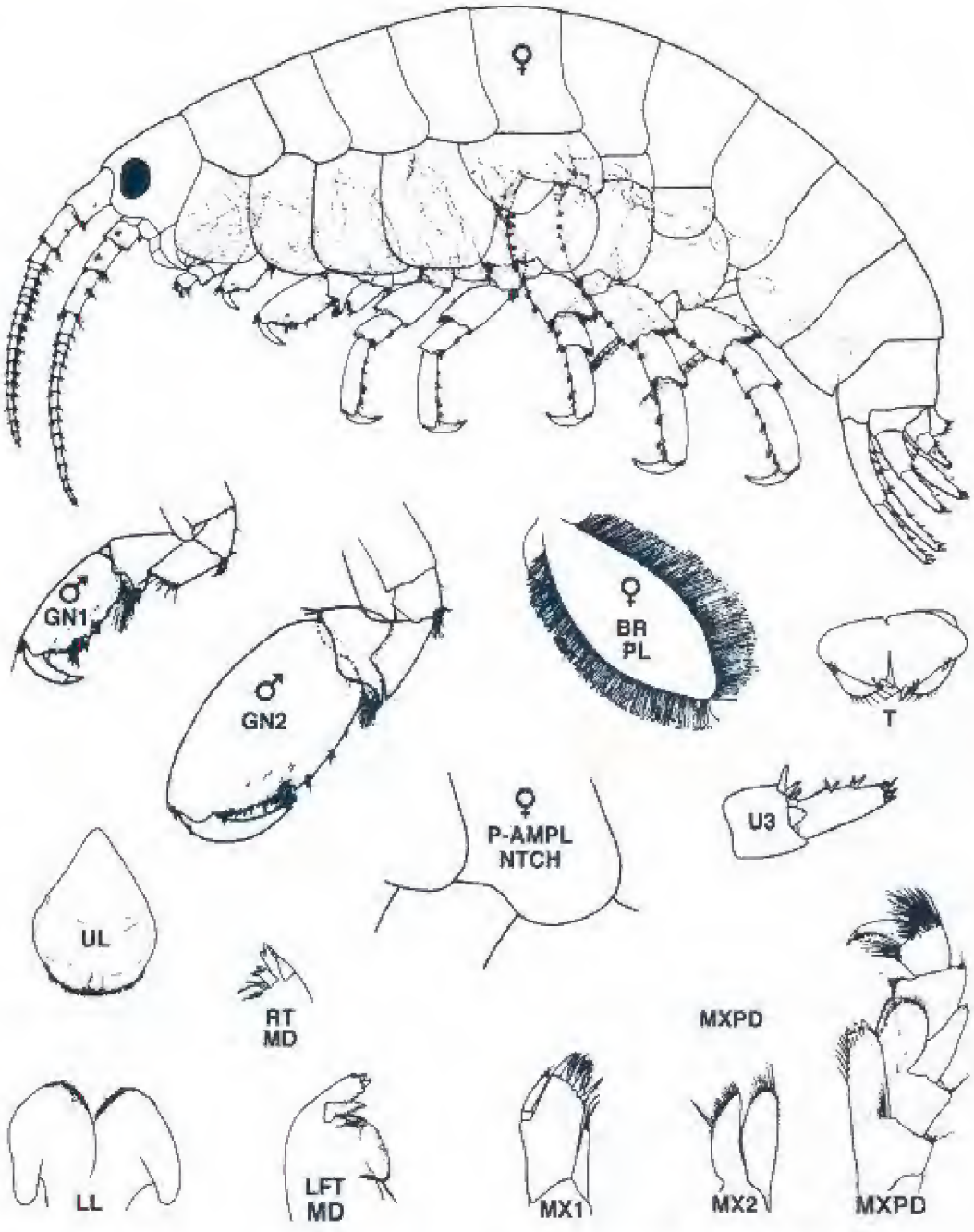

Fig. 23. ***Parallorchestes nuda* n. sp.** Male (12.0 mm); female ov (13.0 mm). Stn. P6, Wickaninnish Bay, Vancouver I., B. C.

ened distally; segment 5 short, segment 6 longer than segment 5. Peraeopods 6 & 7, segment 4 slightly broadened, length nearly equal to segment 6, anterior marginal spines weak to medium.

Epimeral plates 2 & 3, hind corners slightly acuminate, margins nearly bare. Uropod 1, peduncle slightly shorter than rami, outer margin with 3-4 short spines and ordinary distal spine; rami each with 2-3 marginal spines and short apical spines. Uropod 2, outer ramus distinctly the shorter, each with 3 marginal spines. Uropod 3 medium; outer ramus longer than peduncle, with 2 posteromarginal clusters, and apical group of medium spines; inner ramus with small subapical seta.

Telson lobes short, apex rounded, each with single apical spines and 3 short subapical marginal setae.

Brood plate (gnathopod 2), subovate, broadest medially, marginal setae relatively short (~1/2 width of plate). Preamplexing notch a shallow obtuse indentation on anterior margin of the lower lobe of peraeon 2.

Male (12.0 mm). Gnathopod 1, basis with medium strong hydrodynamic lobe; carpal lobe large, margin with numerous long comb setae; propod subrectangular;

dactyl simple, stout. Gnathopod 2, basis with medium srong hydrodynamic lobe; carpal lobe regular distinct; propod relatively small, subovate,palm short. oblique, gently convex.

Etymology: From the Latin "nudus" meaning bare,with reference to the weakly setose antennae.

Distributional Ecology: Known only from the type locality at Moraes beach, Wickaninnish Bay, Vancouver I., B. C; in surf-exposed sand at low water level.

Remarks: *Parallorchestes nuda* differs from *P. minima* in its nearly bare peduncular segments of antenna 1, and in its significantly larger size (to 13 mm).

Parallorchestes zibellina (Derzhavin)
(Fig. 24)

Parhyale zibellina Derzhavin, 1937: 92, Plate IV, fig. 1;—Gurjanova 1951: 815, fig. 569;—Bulycheva 1957: 78, figs. 27a,b.
Parallorchestes zibellina Bousfield 1981: 78, fig. 7;—Barnard & Karaman 1991: 371.

Material Examined:
Sea of Japan, Derzhavin coll., 1926 - 2 ♂♂ (10 mm) (slide mount), 1 ♀ ov (9.0 mm), Zool. Inst. No. 8/29566; Ibid, 2 ♂♂, 3 ♀♀, Zoological Museum No. 29566.

Diagnosis: Male (10 mm). Body medium large, dorsally smooth or nearly so. Peraeon segments with indistinct posterior and ventral marginal thickening. Eye medium, obliquely subovate. Antennae of medium length. Antenna 1, peduncle medium, segments each with 3-4 posterior marginal clusters of setae; flagellum 9-10-segmented, segments posteriorly spinose-setose. Antenna 2, peduncles 3-5 with 1-2 anterolateral marginal clusters of short spines and single posterodistal setal clusters; flagellum 12-13-segmented, segments short setose.

Mandible, left lacinia 5 1/2-dentate; spine row with 2 medium blades. Maxilliped, inner plate, apex obtuse; outer plate with broadly acute inner distal cutting edge; dactyl basally thick, narrowing distally.

Coxal plates 1-4 rounded below; coxae 2-3, hind margins with weak shelf, lacking cusp. Coxa 5 aequilobate. Coxa 6 shallowly posterolobate, anterior lobe sharply rounded below. Coxal gills broadly lobate, largest on peraeopods 5 & 6.

Gnathopod 1 medium strong; basis with small hydrodynamic lobe; carpal lobe medium; propod subovate, broadening distally; palm short,oblique, nearly straight, not sharply demarcated from convex lower margin; dactyl simple, tip closing on paired posterodistal spines. Gnathopod 2, basis and ischium with medium hydrodynamic lobes; carpal lobe narrow; propod large, broadly subovate, palm oblique, nearly straight; dactyl heavy.

Peraeopods 3 & 4 medium, not shortened; segment 4 short; segment 6, posterior margin with 2 stout median spines and short distal clasping spine; dactyls medium strong. Peraeopods 5-7 not shortened, stout; bases relatively narrow, hind margins moderately crenulate, each with small notch and surge seta; segment 6 with 2 stout anterior marginal spines and short distal clasping spine. Peraeopod 5, segment 4 somewhat broadened distally; segment 5, length ~1/2 segment 6. Peraeopods 6 & 7, segment 4 not shortened, as in peraeopod 5, slightly shorter than segment 6.

Epimeral plates 2 & 3, hind corners weakly acuminate, lower margins nearly bare. Uropod 1, peduncle and rami subequal in length, outer margin with 4-5 spines and medium distolateral spine; rami with 3-4 marginal spines and short apical spines. Uropod 2, peduncle short; rami each with 2-3 marginal spines, outer ramus slightly the shorter. Uropod 3 short; peduncle with 2 posterodistal spines; outer ramus not longer than peduncle, with 4-5 medium apical (but no marginal) spines; inner ramus short, apex rounded, smooth.

Telson lobes broad, narrowing distally, each with single apical spine and 4-5 subapical marginal setae.

Female ov (9.0 mm). Antenna 2, peduncular segments more strongly setose than in male. Gnathopod 1, basis and ischium with very weak hydrodynamic lobes; carpal lobe short; propod slender, palm oblique, weakly separated from posterior margin by paired slender spines. Gnathopod 2, basis and ischium with weak hydrodynamic lobes; carpal lobe short, relatively broad; propod subovate, larger and deeper than in gnathopod 1. Brood lamella (gnathopod 2) relatively short, slightly broadening and rounding distally, marginal setae elongate. Pre-amplexing notch a very shallow indentation on the anterodistal margin of peraeon 2.

Distributional Ecology: Northern Sea of Japan, southern Sakhalin Ids. and Sea of Okhotsk, to Kurile Ids., among algae and *Zostera*, LW level to 7 m depth (see Bulycheva 1957, p. 82).

Remarks: *Parallorchestes zibellina* is apparently replaced along the North American Pacific coast, from the Aleutian Islands to Vancouver Island, by a counterpart species, *P. kabatai* n. sp. (below).

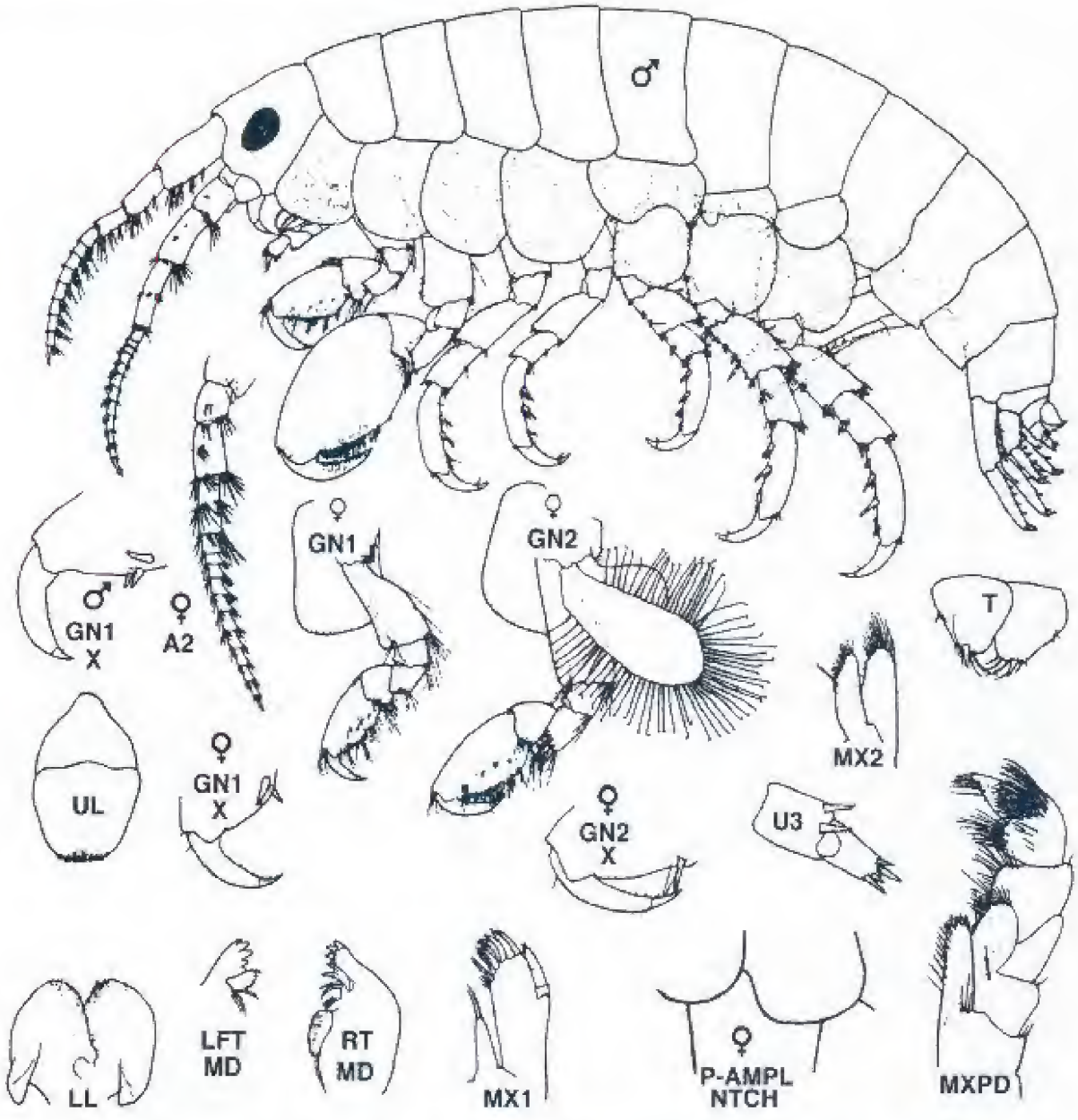

Fig. 24. *Parallorchestes zibellina* (Derzhavin, 1937). Male (10.0 mm); female ov (9.0 mm). Peter-the-Great Bay, Sea of Japan.

***Parallorchestes kabatai* n. sp.**
(Fig. 25)

Parallorchestes occidentalis Bousfield 1981: 78 (nomen nudum);—Bousfield 2001: 104.

Material Examined:
ALASKA
Aleutian Islands: Amchitka I., C E O'Clair Stn 1A-1,, July, 1973 - 1 ♀. Izenback lagoon, Unimak I., LW, N. A. Powell coll. July, 1969 - 1 ♀ ov (10 mm) (slide mount).
Southeastern Alaska: ELB Stn, 1961: A171, Puffin Bay, Baranof I.(56°16'N 134° 48'W), LW, among algae on boulder beach, July 25 - ♂ (10 mm) **Holotype** (slide mount) CMNC 2002-0061; ♀ im (5.0 mm) **Allotype** (slide mount), CMNC 2002-0062; 9 ♂♂, 10 im, **Paratypes,** CMNC 2002-0063.
ELB Stn, 1980: S1B8, NW end of Hogan I., Chichigof I. (57°43'N 136°15.5'W), on rocks under open stones, MW-LW, July 28 - 1 ♂ (9.5 mm) (slide mount), sev. ♂♂, ♀♀.

BRITISH COLUMBIA
S. Vancouver Island: Bordelais Islet, Vancouver I., LW, Ian Lawn coll., July, 1976 - 9 ♂♂, 14 ♀♀, 55 im.

Diagnosis: Male (10 mm). Body medium, dorsally smooth or nearly so, with strikingly variegated colour pattern. Peraeon segments with slight posterior and ventral marginal thickening. Eye medium, broadly ovate. Antennae relatively short, subequal, peduncles

medium. Antenna 1, peduncles 1 & 2 with 2-3, and peduncle 3 with 1 posterior marginal clusters of setae; flagellum ~12-segmented, segments posteriorly setose. Antenna 2, peduncles 3-5 with 1-2 anterior marginal spine clusters and single posterodistal setal clusters; flagellum 13-14-segmented, segments short-setose.

Mandible, left lacinia 5-dentate; spine row with 2 medium blades. Maxilla 2, inner plate with 2 pectinate blades among the apical masticatory setae. Maxilliped, inner plate, apex obtuse; outer plate with broadly acute inner distal cutting edge; dactyl thick.

Coxal plates 2-3 subquadrate, lower margins gently convex, hind margins not cuspate. Coxa 5 aequilobate. Coxa 6 strongly posterolobate, anterior lobe sharply rounded below. Coxal gills broad, largest posteriorly.

Gnathopod 1 medium; basis with small hydrodynamic lobe; carpal lobe small, propod slightly broadening distally, palm short, oblique, nearly straight; dactyl simple, tip closing on paired posterodistal spines. Gnathopod 2, basis and ischium with medium hydrodynamic overlapping lobes; carpal lobe narrow; propod medium, subovate, narrowing distally, palm very oblique, nearly straight; dactyl short.

Peraeopods 3 & 4 medium stout; segment 4 short, <1/2 segment 6; segment 6, posterior margin with stout proximal spine and larger distal medium clasping spine; dactyls medium. Peraeopods 5-7 relatively short, stout; bases broad, hind margins weakly crenulate, each with pronounced notch and surge seta; median clasping spine of segment 6 strong. Peraeopod 5, segment 4 broadened distally; segment 5 short (<1/2 segment 6). Peraeopods 6 & 7, segment 4 short, broadened distally, shorter than segment 6.

Epimeral plates 2 & 3, hind corners acuminate, lower margins weakly spinose. Uropod 1, peduncle and rami subequal in length, outer margin with 2-3 spines and medium long distolateral spine; rami with 1-2 marginal spines and short apical spines. Uropod 2, outer ramus slightly the shorter, rami each with 2 marginal spines. Uropod 3 medium, relatively slender; outer ramus tapering distally, slightly longer than peduncle, with medium apical spines and 1-2 clusters of posteromarginal spines.

Telson lobes broad, rounding distally, each with single apical spine and 4 subapical marginal setae.

Female ov (10 mm). Gnathopod 1 similar to that of male but more slender; basis with small rounded hydrodynamic lobe. Gnathopod 2, basis and ischium with small hydrodynamic lobe; carpal lobe slender; propod subrectangular, deeper than in gnathopod 1 and slightly broadening distally. Brood lamellae regular. Preamplexing notch undeveloped in present material.

Etymology: The patronym recognizes the fundamental contributions of Dr. Zbigniew (Bob) Kabata, Pacific Biological Station, Nanaimo, B. C.,to development of knowledge of the systematics and biology of marine crustaceans.

Distributional Ecology: Aleutian Islands, Alaska, through SE. Alaska to Barkley Sound, Vancouver I.; among algae at LW level, along semi-protected cold-water rocky coasts.

Remarks: *Parallorchestes kabatai* differs from western counterpart *P. zibellina* in its less setose antennae, smaller gnathopods, less strong spination of the uropods, and relatively short and more robust peraeopods.

Parallorchestes asiatica Tzvetkova
(Fig. 26)

Parallorchestes asiaticus Tzvetkova, 1990: 47-53, figs. 7-10.

Material Examined by Tzvetkova.
Gulf of Kronotsk, Olga Bay, 4 m depth, rock bottom, sampler frame, 0.1 m, A. N. Golikov coll., 16 Aug., 1975 - ♂ (10 mm) (**Holotype**), 2 ♀♀ (10, 11 mm) (**Paratypes**), No. 1/82164; Ibid. - 1♂ (7.5 mm), No. 2/82165; Ibid. - boulders with sand, 0.1 m, V. G. Averintsev coll., 16 Aug., 1975 - 2 specimens, No. 3/82166.

Diagnosis. Male (10 mm): Posterior margins of peraeon segments 1-7 and pleon segments 1 & 2 with strongly expressed transverse spindle-shaped thickening. Antennae regular; antenna I, pecluncular segment 2 longer lhan 3, both with small median poslerior matginal seta and posterodistal sctal cluster; flagellum 9-segmented. Antennae 2, peduncular segments 4 & 5 laterally with scattered short spines; flagellunm 12-segmented.

Upper lip slightly notched distally. Mandible, lcft lacinia 5-dentate,spine row with 2 3 blades. Maxilla I reguylar. Maxilla2,plates relativelynarrow. Maxilliped palp well-developed, segments slender.

Coxa 1 broadly rounded anterodistally. Coxa 2 nearly square, lower corners rounded. Coxae 3 with trace of posterior marginal shelf. Coxa 5 slightly posterolobate, hind margin crenulate. Coxal gills medium, sac-like.

Gnathopod 1, basis and ischium with mediun1 hydrodynamic lobes; segment 6 subrectanoular-, palm evenly oblique, sharply demarcated from the posterior margin by two long, pointed locking spines; dactyl thick, slightly exceeding palmar margin, with several short setae on the inner margin, unguis short. Gnathopod

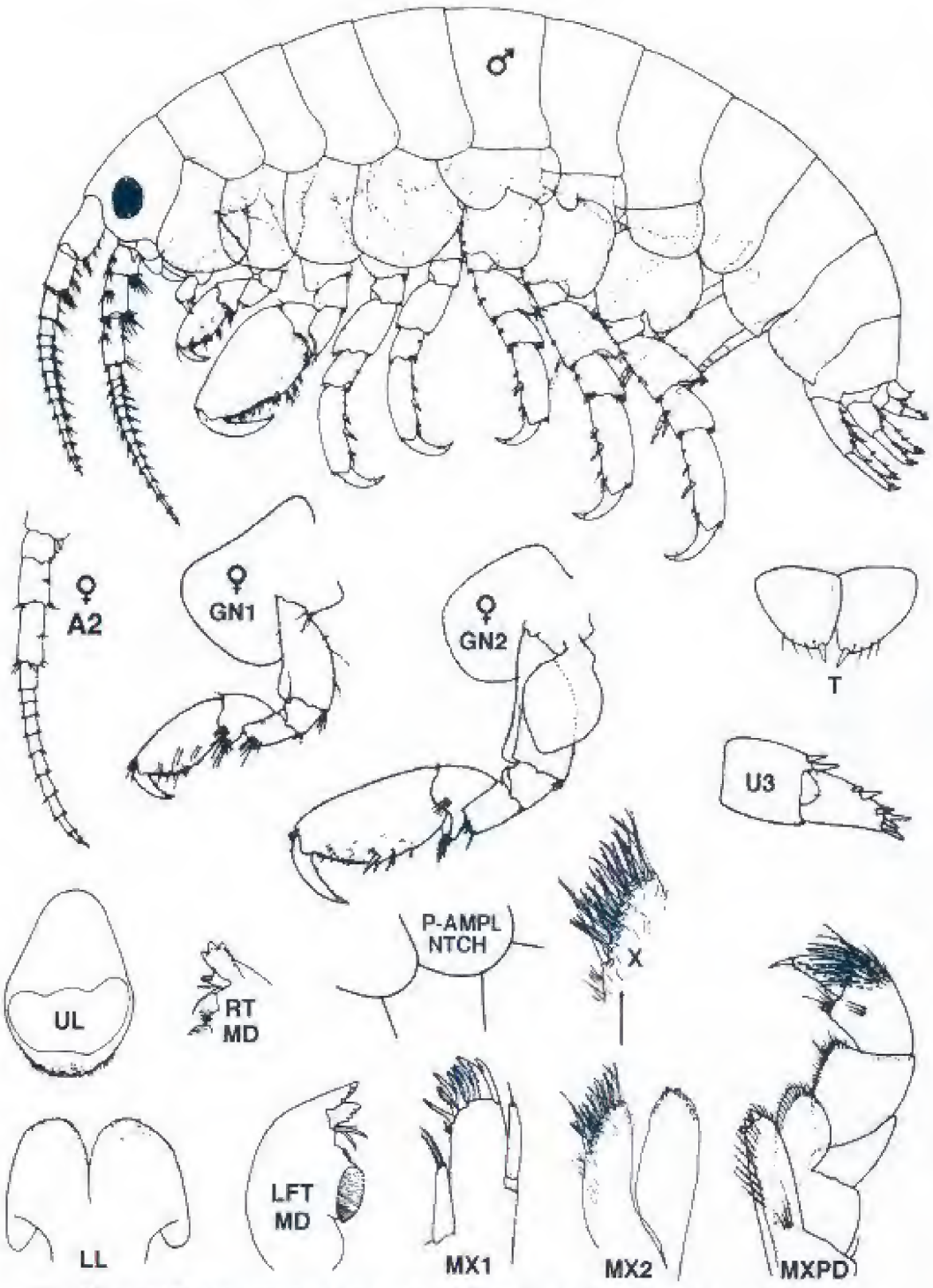

Fig. 25. ***Parallorchestes kabatai* n. sp.** Male (10.0 mm); female im. (5. 0 mm). ELB Stn. A171, Puffin Bay, Baranof I., Southeastern Alaska.

2, basis and ischium each with medium strong hydrodynamic lobe; carpal lobe small, narrow; propod short-rectangular, with nearly parallel anterior and posterior rnargins and evenly sloped palmar margin, sharply defined from the posterior margin by a pair of thick locking spines; dactyl mediun strong, slightly shorter than the palmar margin, inner margin lined with short setules, unguis small.

Peraeopods 3 & 4 regular; segment 5 short; segment 6, hind margin with short striated clasping spines. Peraeopods 5-7 short, stout; posterior margins of bases crenulated, each with distinct notch and surge seta; segment 4 slightly broadened distally; segment 5 short, little longer than wide; segment 6 with 2-3 strong striated anterior marginal spines; dactyl stout, strongly curved, with small subapical seta.

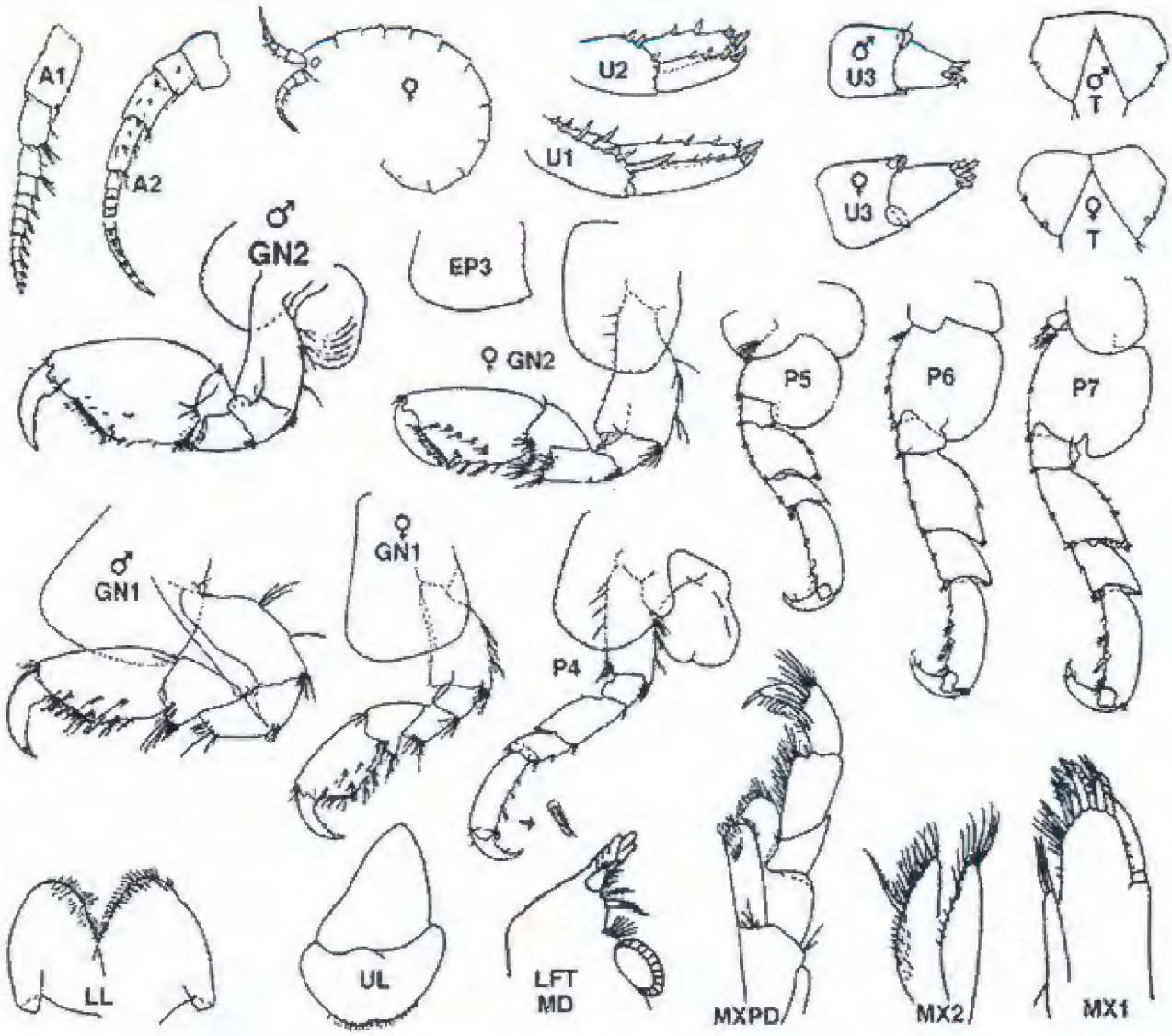

Fig. 26. *Parallorchestes asiatica* Tzvetkova, 1990. Male (10.0 mm); female ov (11.0 mm). Kronotkoi, Kamchatka (modified from Tzvetkova 1990).

Epimeral plates 2 & 3, hind corners acuminate, posterior margins gently sinuous, lower margins weakly spinose. Pleopods regular. Uropod 1, peduncular distolateral spine strong, extending nearly half length of outer ramus; inner and outer ramus with 3 short marginal spines and a few medium apical spines. Uropod 2, rami subequal, each with 2-3 marginal spines. Uropod 3, peduncle thick, with 2-3 posterodistal spines; outer ramus about equal in length to peduncle, with 6-7 apical spines; inner ramus very small, with 1 small seta on inner margin.

Telson lobes apically acute, bearing 1-2 slender apical spines (or spine-like setae) and a few lateral spinules.

Female ov (10-11 mm): Gnathopod 1, hydrodynamic lobe medium on basis, evanescent on ischium; carpal lobe small; propod slightly broadening distally, lower margin with 2 clusters of setae. Gnathopod 2, basis and ischium with medium hydrodynamic lobes; carpal lobe relatively long; propod relatively large, subrectangular, posterior margin with 2-3 clusters of setae. Brood plates typical of the genus (see *P. americana*, fig. 28). Preamplexing notch of peraeon 2 not described.

Distributional Ecology. Known only from Olga Bay, Gulf of Kronotsk, Bering Sea coast of Kamchatka; on sediments and sand at shallow subtidal depths of 4-6 m.

Remarks: The presence of the transverse spindle-like thickenings on the posterior part of the thoracic and I st abdominal segments might suggest a close relationship

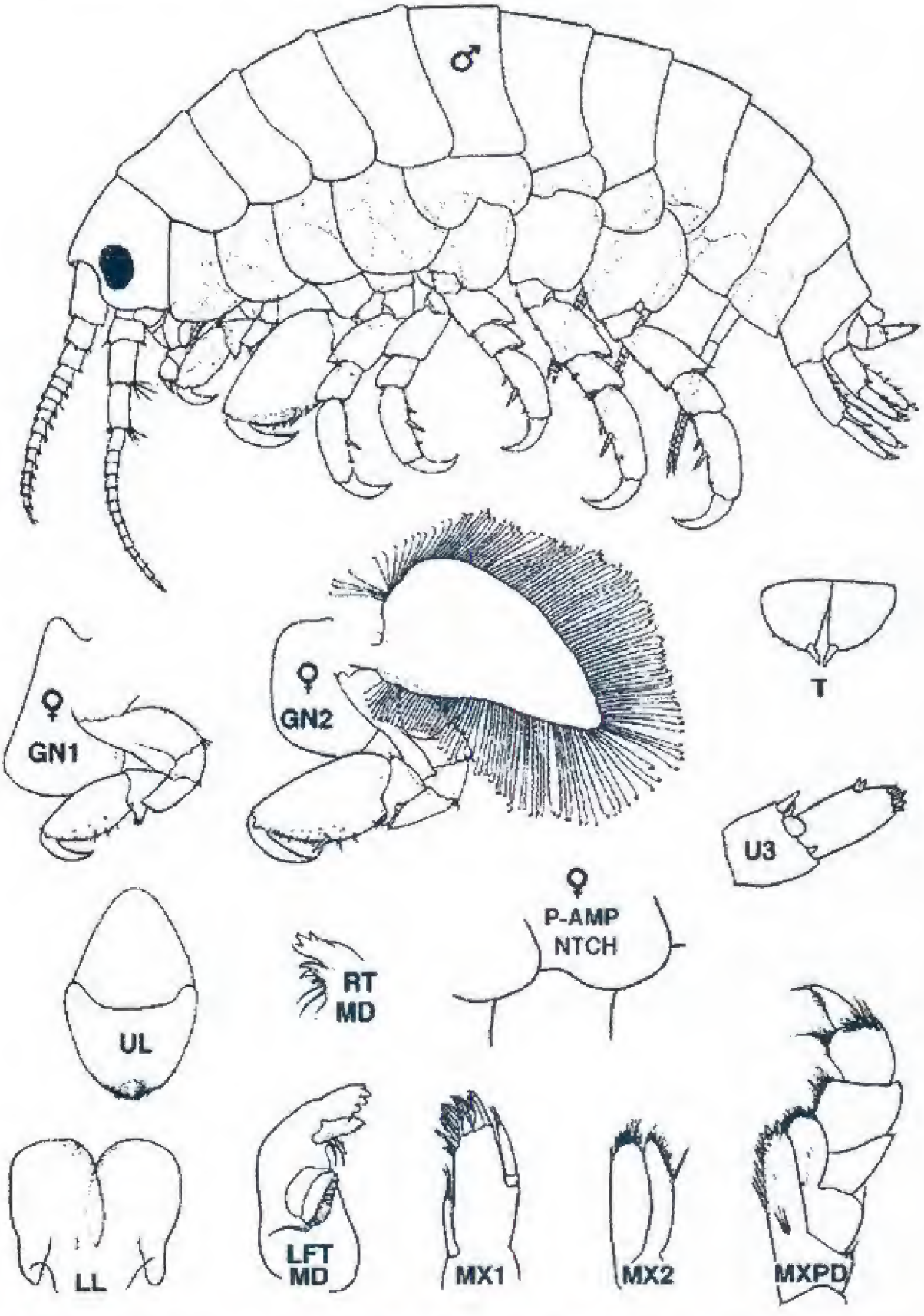

Fig. 27. *Parallorchestes americana* Bousfield, 1981. Male (7.5 mm); female ov (10.0 mm). ELB Stn A171-72, 1961, Puffin Bay, Baranof I., southeastern Alaska.

between *Parallorchestes asiatica* and *P. americana*. However, *P. asiatica* differs markedly in the shape and armature of the telson; the slender form of the maxilliped palp; the distally narrowing mandibular lobes of the lower lip (broadened in *P. americana*); and absence of marginal spines on the relati vely short outer ramus of uropod 3. *P. asiatica* differs also in the distally broadened propod of gnathopod 1, especially in the female; the steeply oblique propodal palmar margin of gnathopods 1 & 2, and strong demarcation from the posterior margin; the longer peduncular segment 2 of antenna 1 (longer than 3); and in the more strongly armed inner margin of the propod (segment 6) of the peraeopods.

Parallorchestes americana Bousfield
(Fig. 27)

Parallorchestes americana Bousfield 1981: 78, fig.7 (nomen nudum);—Tzvetkova 1990: 52;—Bousfield 2001a: 104.

Material Examined:

Southeastern Alaska: ELB Stns, June-July, 1961: **A75**, Kayak, Wingham I. - 2 ♂♂; A151, Islet east of Johnstone Pt. - 1 ♂; A162, mouth Portlock Harbor, Hill I., bedrock tidepool, LW, July 22 - 2 im; A171-72, Puffin Bay, Baranof I. (56°16'N, 134°48'W) among algae on bedrock and boulders, LW, July 25 - ♂ (7.5 mm) **Holotype** (slide mount), CMNC 20023-0064; ♀ ov (10 mm) **Allotype** (slide mount), CMNC 2002-0065; 12 ♂♂, 2♀♀, 16 subadult **Paratypes**, CMNC 2002-0066; A-172, small island, mouth of Puffin Bay, vertical rock face at LW - 1 ♂, 2 ♀♀.

BRITISH COLUMBIA

Vancouver I. ELB Stn, 1959: O17, Midway Rocks, Wickaninnish Bay (49° 03'N, 125°14'W), MW pools on exposed rock faces, Aug. 13-15 - 1 imm.

Lobban Stns, 1971: CL-1030, N. of Quisitis Pt., Wickaninnish Bay - 13 males, 24 ♀♀ and subadults.

JFL Hart Stn 541, 1932, Ross Islets, Deer Group, V.I. - 2 males, 7 ♀♀, 6 subadults.

Ian Lawn Stn, 1976, off Bordelais Islet, LW, June 26 - 2 ♂♂, 4 ♀♀, 28 subadults.

WASH.-OREGON

ELB Stns, July-Aug., 1966: W24, Kalaloch Beach, south of creek mouth - 2 ♀♀; W58 (1 ♀); W61 (1 ♂); W63 (1♂, 1 imm).

CALIFORNIA

Monterey peninsula, P. Glynn coll., 1959 - 1 ♀.

Diagnosis: Male (7.5 mm). Body small to medium. Peraeon segments 1-7 and abdominal segments 1-3 each with posterior raised ridge. Antenna 1, peduncular segment 2 short, little longer than 3; flagellum 12-14 segmented. Antenna 2, peduncular segments 4 & 5 short, with posterodistal setal cluster; flagellum 12-14-segmented.

Mandible: left lacinia 6-dentate; spine row with 2-3 slender blades. Maxilliped, inner plate narrowing, apex subtruncate; outer plate inner distal margin obtusely rounded; palp segment 2 short, broad, distally subtruncate; dactyl stout, nail medium.

Coxae 1-4 relatively shallow, broad, gently rounded below, hind margins lacking posterior shelf. Coxa 5 slightly anterolobate. Coxal gills heart-shaped, smallest on peraeopod 2, largest on peraeopod 6.

Gnathopod 1 small; basis and ischium with strong overlapping hydrodynamic lobes; carpal lobe small; propod subovate, palm shallowly oblique, weakly defined, merging imperceptibly with posterior margin; dactyl barely overlapping paired posterodistal spines. Gnathopod 2, basis and ischium with strong overlapping hydrodynamic lobes; carpal lobe small, narrow; propod subovate, palm oblique, gently convex.

Peraeopods 3 & 4 stout; segment 4 short; segment 6 with strong median clasping spine flanked by smaller proximal and distal spine. Peraeopods 5-7 short, stout; bases medium broad, hind margins crenulate, each with small notch and surge seta; segment 6, anterior margin with stout median clasping spine and smaller flanking spines; dactyls large, stout. Peraeopod 5, segment 4 short, broad; segment 5 very short,<<1/2 segment 6.

Epimeral plates 2 & 3 regular, hind corners slightly acuminate. Uropod 1, peduncle and rami subequal in length, outer margin of peduncle with 3-4 short spines and strong distolateral spine; rami with 2-3 marginal spines and short apical spines. Uropod 2, outer ramus distinctly the longer, each with 2-3 short marginal and apical spines. Uropod 3 medium; outer ramus longer than peduncle, with apical and single cluster of posterior marginal spines; inner ramus short, nearly bare.

Telson lobes each with single apical spines and 4-5 short subapical marginal setae.

Female ov (10.0 mm). Gnathopod 1 similar to but more slender than that of male. Gnathopod 2, propod relatively large powerful, similar to but smaller than male. Brood plates large, broad, tapering distally and sharply rounded apically; marginal setae long (>1/2 plate width. Preamplexing notch a shallow indentation of the anterior margin of the lower lobe of peraeon segment 2.

Etymology: The term "americana", not derived in the initial reference to the name, alludes to the North American Pacific distribution of the species.

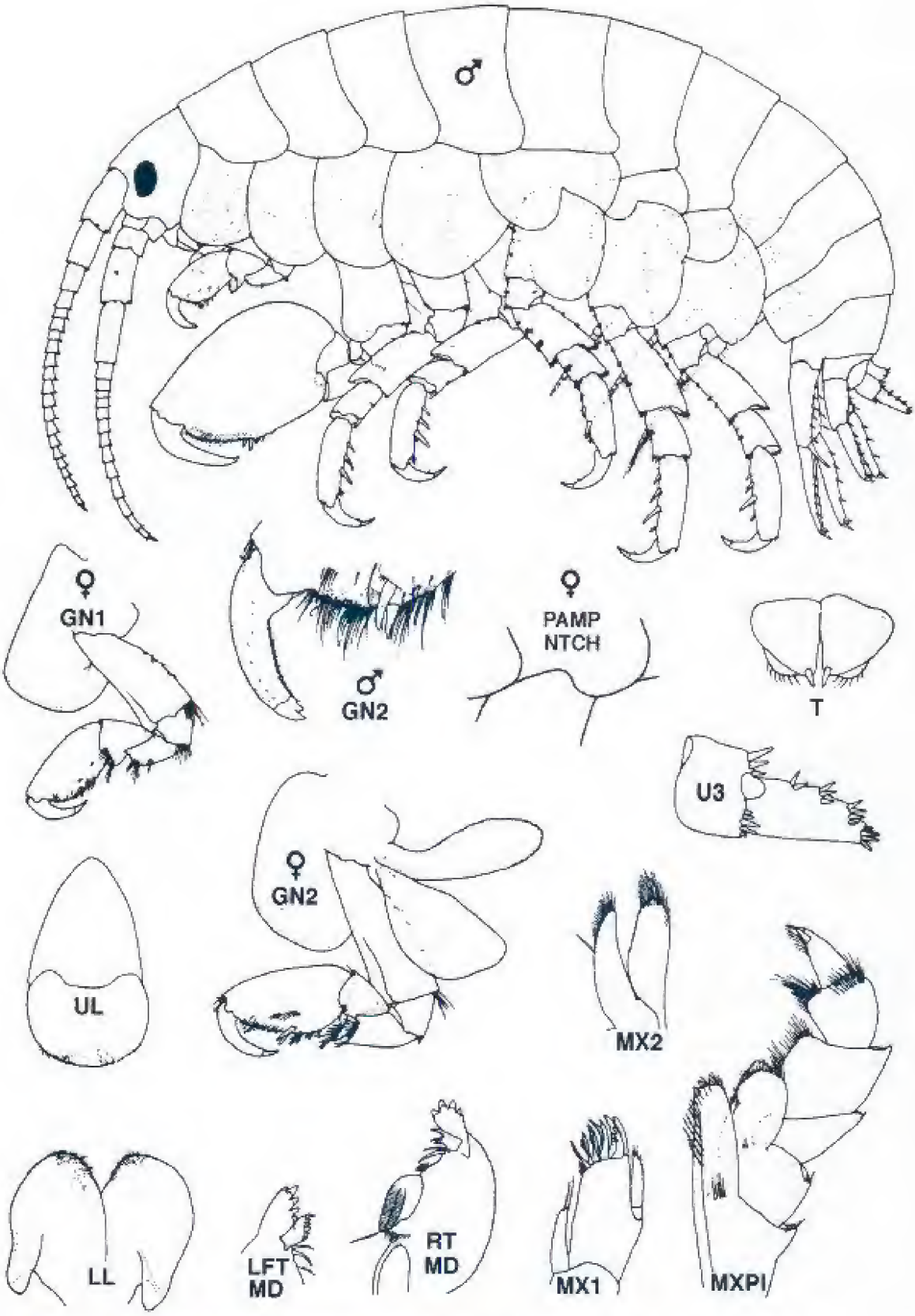

Fig. 28. ***Parallorchestes trispinosa*** **n. sp.** Male (12.0 mm); female br. II (11.0 mm). JFL Hart Stn 2231-14, Estevan Pt., Vancouver I., B. C.

Distributional Ecology: Freely swimming among littoral marine algae and *Phyllospadix*, along surf-exposed coasts, from Prince William Sound, southeastern Alaska, to Oregon and central California.

Remarks: *Parallorchestes americana* differs from its western Pacific counterpart, *P. asiatica*, in character states detailed by Tzvetkova (1990), and summarized in the key (p. 38).

***Parallorchestes trispinosa* n. sp.**
(Fig. 28)

Parallorchestes trispinosa Bousfield, 1981: 78, fig 7 (nomen nudum); — Bousfield 2001: 104.

Material Examined:
BRITISH COLUMBIA
S.outhern Vancouver I.: JFL Hart Stn 2231-14, Estevan Pt., Clayoquot I. (49° 23'48" N, 126° 34'18" W), May 14, 1934 - ♂ (12 mm) **Holotype** (slide mount), CMNC 2002-0067; ♀ (br. II) (11 mm) **Allotype** (slide mount), CMNC 2002-0068; ♂ **Paratype,** CMNC 2002-0069.

Diagnosis: Male (12.0 mm). Body medium large, dorsally smooth or nearly so. Antennae medium long, peduncles well developed, lacking posterior marginal spines. Antenna 1, flagellum 18-20-segmented. Antenna 2, peduncles 4 & 5 smooth; flagellum relatively short, 15-18 segmented.

Mandible, left lacinia 6-dentate; spine row with 2-3 slender blades. Maxilliped, apex of inner plate gently rounded; outer plate, cutting inner distal margin squared; palp segment 2 broad, distally truncate; dactyl stout.

Coxal plates 1-4 large, broad, rounded below, lacking trace of posterior marginal shelf. Coxa 5 relatively large, slightly anterolobate. Coxa 6 shallowly posterolobate. Coxal gills broadly lobate, somewhat reverse L-shaped, largest on peraeopod 5.

Gnathopod 1 relatively small; basis with small anterodistal lobe, lacking on ischium; carpal lobe short; propod subrectangular; palm short, very oblique, convex, weakly demarcated from posterior margin; dactyl, hind margin lined with fine setules, unguis unequally bifid at apex, closing on stout paired posterodistal spines. Gnathopod 2 large, powerful; basis and ischium with strongly overlapping hydrodynamic lobes; carpal lobe small, cryptic; propod very large, subovate, narrowing slightly distally, palm short, oblique, convex near hinge; dactyl relatively short, narrowing distally.

Peraeopods 3 & 4 stout; segment 6, posterior margin with 3 stout distally enlarging spines; dactyls large. Peraeopods 5-7 stout; bases broad with weakly crenulate convex hind margins, each with distinct notch and surge seta; segment 5 short, length about 1/2 segment 6 propod with 3-4 stout, anterior marginal spines, penultimate spine strongest. Peraeopod 5, segment 4 slightly broadened, nearly as long as segment 6. Peraeopods 6 & 7, segment 4 little broadened, subequal in length to segment 6; dactyls stout, strongly curved.

Epimeral plates 2 &3, hind corners nearly square, lower margins bare. Uropod 1, peduncle slightly shorter than rami, outer margin with 5-6 spines and medium posterodistal spine; inner ramus with 3-4 marginal spines; outer ramus with 4-5 closely set marginal spines and short apical spines. Uropod 2, rami distinctly longer than peduncle, outer ramus very slightly the shorter, each with 3-4 marginal spines. Uropod 3, outer ramus nearly twice length of short peduncle, with 3 clusters of posterior (upper) marginal spines and short spines on rounded apex; inner ramus very small, rounded, with minute apical seta.

Telson lobes narrowing, each with single apical spine and 5-6 subapical marginal setae.

Female, br. II. (11.0 mm). Gnathopod 1, hydrodynamic lobe of basis medium strong, lacking on ischium; carpal lobe short; propodal palm convex, shallowly oblique, weakly demarcated from posterior margin. Gnathopod 2, hydrodynamic lobe of basis weak, lacking in ischium; carpal lobe narrow, deep; propod larger and paired palmar spines stronger than in gnathopod 1. Brood lamellae plate-like, broadening distally. Preamplexing notch medium deep, slightly obtuse; posterior lobe about two-thirds width of peraeon segment 2.

Etymology: From " tri" + the Latin root "spinosus", with reference to the three groups of posterior marginal spines of the ramus of uropod 3.

Distributional Ecology: Known only from the type locality, a surf-exposed headland of Vancouver Island.

Remarks: Distinctive character states include a bifid unguis of gnathopod 1 (♂), a strong striated clasping spine on the propod of peraeopds 3-7, and an elongate marginally spinose outer ramus of uropod 3. The first is similar to that of advanced species within the genus *Allorchestes* (Hyalellidae) and the second to that within genus *Hyale* (sens. str.). Since *Allorchestes* and *Hyale* differ from *Parallorchestes* in several generic character states (e.g., 1-segmented palp of maxilla 1, uniramous uropod 3, unarmed telson lobes), commonality of bifid gnathopod unguis and stout pereopodal clasping spine may be instances of homoplasious convergence in phyletically unrelated hyalids of similar life styles.

Protohyale n. g.

Hyale (part): Stebbing 1906: 559;—Stout 1913: 650;—Bulycheva 1957: 83.—Barnard 1979: 98, key;—Bousfield 1981: 76, figs. 9, 10;—Krapp-Schickel 1993:728, key:—Barnard & Karaman 1991: 367.
Talitroidea (part) Barnard 1969a: 469.
Protohyale Bousfield 2001a:104.

Type species: *Hyale frequens* Stout, 1913: 650.

Subgenera: ***Protohyale*** nominate subgenus (p. 79); ***Boreohyale*** n. subg.(p. 61); ***Leptohyale*** n. subg. (p. 88); ***Diplohyale*** n. subg. (p. 90).

Diagnosis: Body medium to small, smooth. Eyes round, lateral, small to medium. Antenna 1, peduncle and flagellum short. Antenna 2, peduncle short; flagellum usually elongate, 25+ segmented, proximal segments often with very short setae.

Mandibular left lacinia mostly 5 (6)-dentate; spine row with 3-6 blades. Maxilla 1 palp long, 1-segmented, extending beyond base of apical spines of outer plate. Maxilla 2, inner marginal plumose setae short. Maxilliped, inner plate subrectangular; outer plate distally rounded; palp regular, segment 2 not broader than long; dactyl finely pectinate, with medial marginal setae, rarely sexually dimorphic (terminal whip seta (♂)).

Coxae 1-3 with weak posterior shelf. Coxa 1 not (or slightly) distally broadened. Coxa 4, margin of posterior excavation may have weak obtuse cusp.. Coxa 5 aequilobate (weakly anterolobate to weakly posterolobate. Coxae 6 and 7 shallowly posterolobate. Coxal gills subovate, largest posteriorly.

Gnathopod 1 (♂) larger than, but mostly similar in form to ♀, occasionally dimorphic; hydrodynamic lobes of basis and ischium often well developed; carpal lobe distinct, relatively broad; propod subrectanglar, usually with 2-3 prominent anterodistal spine(s), posterior margin variously setose; palm distinct, oblique, dactyl simple-tipped. Gnathopod 2(♂) powerfully subchelate, regular; hydrodynamic lobe of basis and ischium well developed; carpal lobe lacking; propod subrectangular to subovate, narrowing distally, palm short, oblique.

Peraeopods 3-7, various, usually not stout; bases medium broad, rounded hind margin not strongly crenulated, usually with notch and surge seta; clasping spine(s) distinct, not conspicuously enlarged; dactyls medium strong, inner marginal seta weak or lacking.

Epimeral plates weakly armed, hind corner produced, plate 2 deepest. Pleopods well developed, rami normal. Uropod 1, peduncle shorter than rami, with strong distolateral spine; rami marginal setae few or lacking. Uropod 2 rami unequal, marginal spines few. Uropod 3 short, lacking inner ramus; ramus shorter than peduncle, with apical spines only.

Telson lobes triangular, usually longer than wide, apical margins smooth.

Female: Gnathopod 2 usually similar to, but larger than gnathopod 1. Brood lamellae rounded to narrowly ovate, marginal setae long, hook-tipped. Preamplexing notch pronounced, with unguisial groove.

Etymology: From the Greek *"protos"* meaning first, or earliest form of, and *"hyale"*, alluding to several plesiomorphic character states of component species.

Distributional Ecology: Component species are mainly free-swimming in the swash zone, low intertidal to shallow subtidal, in temperate to warm-temperate marine waters world wide.

Remarks: Genus *Protohyale* is clearly separable from genus *Hyale* by character states utilized in the key to genera (p. 36). Species of both genera are swimmers, but those of *Hyale* possess the more advanced character states of posterior marginal cusps on coxae 2 & 3, and loss of peduncular distolateral spine of uropod 1.

P. (Boreohyale) n. subg.

Type species: ***P. (Boreohyale) lamberti*** n. sp.

Species: ***P. (Boreohyale) hiwatarii*** **n. sp.**; ***P. (B.) jarrettae*** **n. sp.**; ***P. (B.) lamberti*** **n. sp.**(+ varieties); ***P. (B.) neorionensis*** **n. sp.**; ***P. (B.) oclairi*** **n. sp.**; ***P. oculata*** **n. sp.**; ***P. (B.) seticornis*** **n. sp.**

Extralimital species: *Protohyale (Boreohyale) camptonyx* (Heller,1866); *P. (B.) grenfelli* (Chilton, 1917); *P. (B.) loorea* Barnard, 1974; *P. (B.) maroubrae* (Stebbing, 1899); *P. (B.) pumila* (Hiwatari & Kajihara, 1981a); *P. (B.) rubra* (Thomson, 1879)(see Hurley 1957, fig. 3); *P. (B.) wilari* (Barnard, 1974); *P. (Boreohyale)* sp. (= *Hyale schmidti* Iwasa 1939); *P. (Boreohyale)* sp. (= *Hyale dollfusi* Bulycheva 1957).

Diagnosis: Antenna 1, peduncular segment 2 not reduced, longer than peduncular segment 3.

Mandibular left lacinia 5-6 dentate; right lacinia tricuspate. Maxilla 2, inner plate with 6-10 strongly pectinate apical setae. Maxilliped palp not sexually dimorphic.

Coxae 1-4. posterior marginal shelf weak or lacking; Coxa 4, margin of posterior excavation lacking median cusp. Coxal gills large, sac-like.

Gnathopod 1, basis and ischium, hydrodynamic (anterodistal) lobe usually lacking or evanescent (both sexes); dactyl normal.

Peraeopods 3-7, segment 6, inner margin variably spinose, clasping spine (when present) single or striated. Peraeopods 5-7, bases broadly rounded, each with posterior marginal notch and surge seta.

Epimeron 1, hind corner not smoothly rounded. Uropod 1, distolateral peduncular spine short, length less than one-third length of outer ramus. Uropod 3, peduncle usually with two posterodistal spines.

Female: Brood plate (gnathopod 2), apex rounded to subacute. Preamplexing notch distinct, with short, narrow, oblique or curved unguisial notch.

Protohyale (Boreohyale) lamberti n. sp.

(Fig. 29)

Hyale frequens Barnard 1954: 23 (Oregon);—Bousfield 1981: fig. 10;—Austin 1985: 594;—Staude 1987: 379, fig. 18.34;
Hyale frequens (part) Barnard & Karaman 1991: 370;—Bousfield 2001a: 104.
Hyale rubra frequens Barnard, 1969b: 139 (part?)
not *Hyale frequens* (Stout, 1913): 650 (Laguna Beach)
not *Hyale frequens* Barnard 1962 (S. California)\

Material Examined: ~1440 specimens in 82 lots, SE Alaska to Oregon. ELB Station references: Bousfield (1958, 1963, 1968); Bousfield & McAllister (1962); Bousfield & Jarrett (1981).

ALASKA

Southeastern Alaska: ELB Stns, 1961: A6 (2), A22 (8), A57 (8), A80 (30), A129 (1), A147 (1), A164 (14), A171 (6). ELB Stns, 1980: S4B4 (1 ♀), S4B5 (4 spms); S5B7 (1 ♂, 3♀♀).

BRITISH COLUMBIA

Queen Charlotte Islands: ELB Stns, 1957: E2 (11); W1 (6), W8 (17), W11 (2), W12 (16), W15 (4).
North Central Coast: ELB Stns., 1964: H2 (1), H12 (8), H32 (5), H33 (18), H35 (4), H50 (6), H53 (56), H57 (9).
South Central Coast: ELB Stns., 1955: M11 (1).
Northern Vancouver Island: ELB Stns, 1959: N1 (27); O1 (3), O2 (1), O5 (19), O11 (28), O12 (8), O17 (21); V4b (12), V5 (9), V6 (1), V10 (1), V17 (2).
Southern Vancouver Island: ELB Stns., 1955: F1 (62), F2 (5), F5 (11); P4 (7), P5b (12), P6 (8), P7 (41), P9 (7); G11 (7).
ELB Stns, 1964: H43 (7), H44 (96).
ELB Stns., 1970: P703 (2), P710 (52), P711, Brady Beach, bedrock, algae, LW, July 20 - 3 ♂♂ (7.8 mm)(1 slide mount), CMNC 1983-1533; 1 ♀ ov; P712 (1), P714 (22), P715 (65), P719 (85).
ELB Stns., 1975: P3a,b (11), P5a,d (12), P17 (132), P20 (22), P21a (9).
ELB Stns. 1976: B11b (1), B28 (15).
ELB Stns. 1977: B5 (2), B6a, Trial I. Point, Victoria, bedrock, algae, LW, May 18 - ♂ (9.0 mm) **Holotype** (slide mount), CMNC 2002-0073; ♀ ov (7.5 mm) **Allotype** (slide mount), CMNC 2002-0074 - 22 ♂♂ ♀♀ **Paratypes**, CMNC 2002-0075; B11b (1), B12 (9), B19a,b (59).
Additional British Columbia material: Ucluelet, C. S. Young & W. Spreadborough, aummer, 1909 - 6 spms; Gonzales Pt., J. F. L. Hart, 1941 - 1 ♂, 2 ♀♀ ov; Botany Beach, Port Renfrew, V. I., R. K. Lee, 1971 - 1 ♀, 1 im; Whiffen Spit, Sooke Hbr., R. K. Lee coll., 1973 - 1 ♀ ov

WASH-OREGON

ELB Stns. July-Aug., 1966: W34 (13), W35 (6), W36 (18), W40 (23), W42 (15), W57 (5), W60 (7), W63 (1).
Eagle Cove, San Juan I., R. M. O'Clair Stn. 740011, 1974 - 1♂, 2 ♀♀.
KE Conlan Stn, Sunset Bay, ORE, 1986 - 184 spms (incl. *P. seticornis*).

Diagnosis: Male (9.0mm): Eyes medium to medium large, circular. Antenna 1, peduncular segment 2 distinctly longer than 3; flagellum with 13-15 seg-

Key to subgenera of *Protohyale* n. g.

1. Gnathopod 1 (♂), dactyl bifid or double pronged ..... ***Diplohyale*** (p. 90)
   Gnathopod 1 (♂), dactyl regular, not double pronged ..... 2.

2. Maxilliped palp slender and strongly sexually dimorphic ..... ***Leptohyale*** (p. 88)
   Maxilliped palp normal, if sexually dimorphic, male unguis a whip seta ..... 3.

3. Antenna 1, peduncular segment 2 short, little longer than segment 3; gnathopod 1 with hydrodynamic lobes of basis and ischium strong (♂) ..... ***Protohyale*** (p. 79)
   Antenna 1, peduncular segment 2 longer than segment 3; gnathopod 1, hydrodynamic lobes of basis and ischium weak or lacking (♂) ..... ***Boreohyale*** (p. 61)

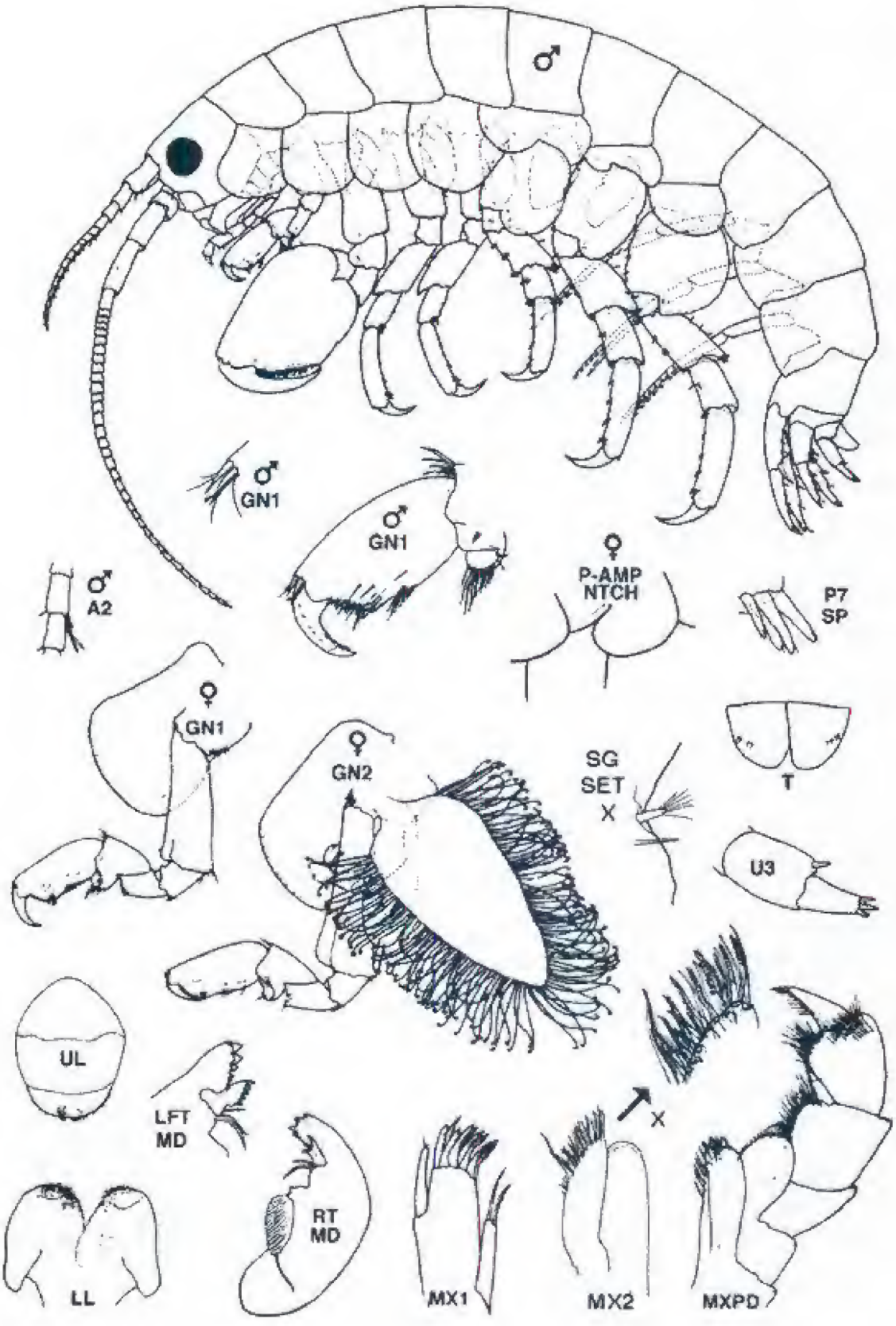

Fig. 29. *P. (Boreohyale) lamberti* n. sp. ♂ (9.0 mm); ♀ ov (7.5 mm). ELB Stn. B6a, Trial I. Point, Victoria, B. C.

Key to North Pacific species of subgenus *Boreohyale*

1. Uropod 1, outer ramus with 0-2 marginal spines . . . . . 2.
   Uropod 1, outer ramus with 3-5 marginal spines . . . . . 4.

2. Eye large, antenna 2, flagellum short (<20 segments); uropod 3, ramus short, length not> 1/2 peduncle . . . . . ***P. (B.) oculata*** n. sp. (p. 70)
   Eye medium; antenna 2, flagellum elongate (>25 segments); uropod 3, length of ramus >1/2 peduncle . . . . .3.

3. Gnathopod 1 (♂) , propod slender rectangular; peraeopods 6 and 7, dactyls short . ***P. (B.) oclairi*** n. sp. (p. 71)
   Gnathopod 1 (♂) propod deep rectangular; peraeopod dactyls long strong . . . *P. (B.) pumila* (H. & K.) (p. 77)

4. Peraeopod 5, segment 5 short, (W=L.); . . . . . 5.
   Peraeopod 5, segment 5 regular (L> W) . . . . . 6.

5. Antenna 2, flagellum 30+ segmented, segments bare; peraeopods 5-7 regular, slender, anterior margins weakly spinose . . . . . ***P. (B.) lamberti*** n. sp. (p. 62)
   Antenna 2 flagellum ~25-segmented, basal segments short-setose; peraeopod 5-7, segments stout, anterior margins spinose . . . . . ***P. (B.) neorionensis*** n. sp. (p. 76)

6. Gnathopod 1 (♂), palm shallow, continuous with posterior margin; telson lobes short, not longer than wide . . . . . *P. (Boreohyale)* sp. Bulycheva (p. 79)
   Gnathopod 1 and telson not so . . . . . 7.

7. Peraeopods 6-7slender, distinctly longer than 3-5, segment 4 slender (length > 2X width) . . . . . ***P. (B.) jarrettae*** n. sp. (p. 65)
   Peraeopods 6-7 relatively stout little longer than 3-5; segment 4 broadened (length < 2X width) . . . . . 8.

8. Antenna 1, flagellum with short setae; peraeopods 5-7 heavily spinose . . . . . *P. (B.) hiwatarii* n. sp. (p. 74)
   Antenna 1, flagellar segments with long setae; peraeopods 5-7 regularly spinose. . . . . ***P. (B.) seticornis*** n. sp. (p. 67)

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ments, each bearing 2 aesthetascs. Antenna 2 medium, more than twice length of antenna 1; flagellum with 30-33 segments, setal brushes very weak, inconspicuous.

Upper and lower lips regular. Mandible, left lacinia 5-dentate; spine row with 2-3 accessory blades. Maxilla 1, palp elongate, tip reaching nearly one-half length of apical spine teeth of outer plate. Maxilla 2, inner plate with inner row of ~9 pectinate setae. Maxilliped palp medium broad; dactyl slightly shorter than segment 3, unguis short.

Coxae 1-4, posterior marginal cusp lacking, posterior marginal shelf weak on coxa 1, stronger on coxae 2 and 3, lower margins rounded regular. Coxa 5 aequilobate. Coxal gills sac-like, largest on peraeopod 5.

Gnathopod 1, anterodistal lobe weakly rounded on basis; very weak on ischium; carpus lobe medium, with ~10 marginal comb setae; propod subrectangular,with 2 anterodistal spines, palm short, oblique, posterior angle defined by a pair of short spines, distal portion of posterior margin with single group of setae; dactyl stout, with minute posterior marginal setules,unguis slightly overlapping palm. Gnathopod 2, basis and ischium each with strong, slightly overlapping, hydrodynamic lobes; merus weakly extended posterodistally; carpal lobe lacking; propod subrectangular, anterior margin with 1-2 proximal spines, lower margin nearly bare, palm oblique, with slight hinge tooth, shorter than smooth posterior margin; dactyl regular.

Peraeopods 3-4, segment 5 short; segment 6, posterior margin with 3 -4 weak spines, increasing distally; dactyl relatively slender. Peraeopods 5-7, basis variously broadened, hind margins crenulate, rounded, with notch and surge seta; segment 4 slightly broadened; segment 5 short (~1/2 segment 6); segment 6 (propod) with 4 weak, anterior marginal spines, clasping (locking) spine weak.

Epimeral plates 1-3, hind corners weakly acuminate. Pleopods 1-3 regular. Uropod 1, peduncle with 3-4 outer marginal spines; distolateral spine stout, ~1/3 length of outer ramus; ramus with 3-4 marginal and weak apical spines. Uropod 2, rami unequal, each with 2 marginal spines. Uropod 3, peduncle slightly longer than ramus, with 1-2 posterodistal short spines; ramus tapering, apex blunt, with 3-4 short spines.

Telson, lateral margin of each lobe with small setae.

Female ov (7.5 mm.): Gnathopod 1, hydrodynamic lobe on basis weak, sharply rounded, lacking on ischium; carpal lobe medium, with ~8 marginal comb spines; propod subrectangular, palm short, oblique; dactyl slightly overlapping paired palmar spines. Gnathopod 2 similar to gnathopod 1 but hydrodynamic lobe of basis slightly larger; propod slightly larger, with 2 groups of posterior marginal setae; dactyl not overlapping palm. Brood plate (gnathopod 2) broadly subtriangular, distally sharply rounded, margins with 100+ hooked setae of medium length (<1/2 brood plate width). Pre-amplexing notch short, sharply incised; unguisial groove narrow, short, nearly straight; peraeonal posterodistal lobe broad, smoothly rounding anteriorly.

Etymology: The species is named in recognition of Philip M. Lambert, Royal British Columbia Museum, Victoria, for his dedicated career contribution to the teaching, display, communication and research in marine systematics and ecology.

Distributional Ecology: Southeastern Alaska and northern British Columbia to Oregon to Central California, associated with marine algae (Barnard 1969b) Dominant among seaweed at the low water level.

Remarks: *P. lamberti*, type species of subgenus *Boreohyale*, differs consistently from the type species *frequens* of subgenus *Protohyale* (p. 79) in characters of the subgeneric key (p. 64), especially its stronger peduncular segments of antenna 1, hydrodynamic lobes of gnathopod 1 that are weak or lacking in both males and females, and squared posterior epimeral plate 1.

Some morphological variation was noted in material from localities in British Columbia. Thus, mature males at Brady Beach and Trial I. showed slight differences in degree of brush setation and length of flagellum of antenna 2, in spination and setation of peraeopods 5-7, and in relative length of the ramus of uropod 3. These are not considered of species level significance.

Protohyale (Boreohyale) jarrettae n. sp.

(Fig. 30)

Hyale intermedia Bousfield, 1981: 80 (nomen nudum); *Protohyale intermedia* Bousfield 2001: 104.

Material Examined: ~750 specimens in 42 lots, SE Alaska to Washington State. ELB station references: Bousfield (1958, 1963, 1968), Bousfield & McAllister (1962); Bousfield & Jarrett (1981).

ALASKA

Southeastern Alaska: ELB Stns, 1961: A3 (1), A67 (1), A115 (1).

ELB Stn, 1980: S4B4 - 1 ♀ (photo'd).

BRITISH COLUMBIA

Queen Charlotte Islands: ELB Stns. 1957: E5 (2), E14c (1), E24 (6).

North Central Coast: ELB Stns, 1964: H1 (102), H5 (2), H10 (1), H13 (4), H16 (18), H23 (4), H29 (90), H33 (43), H35 (198), H48 (1), H50 (1), H65 (6).

Northern Vancouver Island: ELB Stns, 1959: O1 (6); V4A (4).

Southern Vancouver Island: ELB Stns, 1955: F2 (2).

ELB Stns, 1964: H44 (1).

ELB Stns, 1970: P703 (11), P710 (16), P711, Brady Beach, Trevor Channel (48°48'48"N, 125° 09'30"W), LW, July 20, 1970 - ♂ (7.5 mm) **Holotype** (slide mount), CMNC 1983-1509, ♀ ov (7.0 mm) **Allotype** (slide mount), CMNC 1983-1510; 51 spms **Paratypes**, CMNC 1983-1511; P715 (1).

ELB Stn, 1975: P17c (2).

ELB Stn, 1977: B4 (19).

Additional British Columbia material: Wouwer I., Barkley Sound, P. Lambert coll., 1973 - 1 ♀, 2 imms; Ibid., Gibraltar I. - 1 ♂.

WASH-OREGON

ELB Stns. July-Aug., 1966: W5 (26), W8 (1), W35 (3), W36 (1), W40 (2), W42 (5), W57 (2), W60 (1); Limestone Pt., San Juan, R. I. Smith coll., 1955 - 4 spms.; Ibid., Kanaka Bay, - 1 spm.

Diagnosis: Male (7.5 mm.): Eyes medium, subcircular. Antenna 1, peduncular segment 2 distinctly longer than 3; flagellum with 14-15 segments, each slightly setose and bearing 2 aesthetascs. Antenna 2 medium, about twice length of antenna 1; flagellum with 26-27 segments, proximally with fine setal brushes.

Upper and lower lips regular. Mandible, left lacinia 5-dentate; spine row with 2-3 accessory blades. Maxilla 1, palp elongate, tip reaching about 1/3 length of apical spine teeth of outer plate. Maxilla 2, inner plate with inner row of pectinate setae. Maxilliped palp relatively slender; dactyl as long as segment 3, unguis medium.

Coxae 1-4, posterior marginal cusp lacking, posterior marginal shelf weak on coxae 1-3, lower margins rounded regular. Coxa 5 aequilobate. Coxal gills sac-like, largest on peraeopod 5.

Gnathopod 1, anterodistal lobe weak but broadly rounded on basis; virtually lacking on ischium; carpus lobe medium broad, with ~15 marginal comb setae; propod short, subrectangular, with 2 anterodistal spines, palm short, convex, oblique, posterior angle defined by

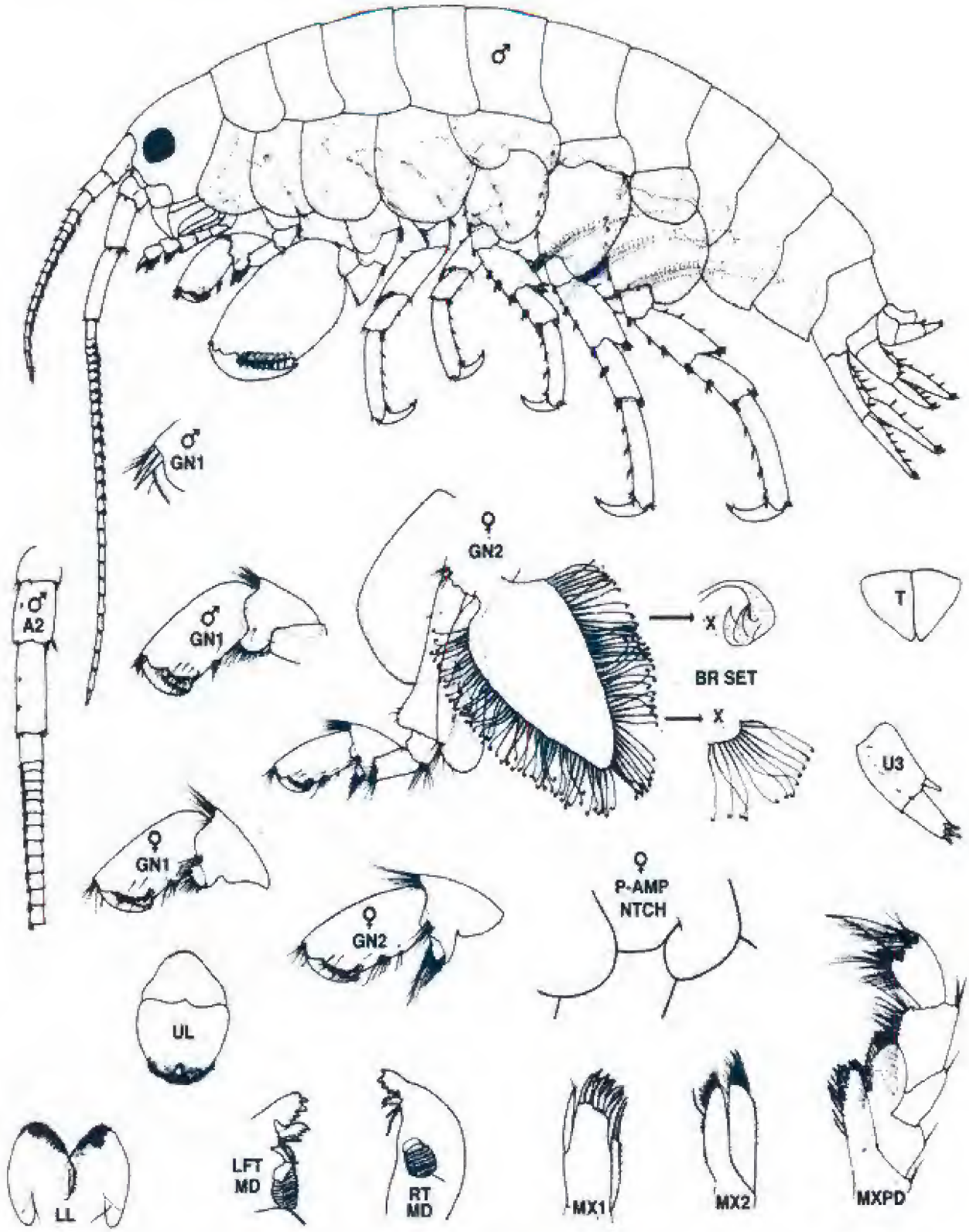

Fig. 30. ***P. (Boreohyale) jarrettae* n. sp.** Male (7.5 mm); female ov (7.0mm) Brady Beach, Trevor Channel, B. C.

a pair of short spines, distal portion of posterior margin with single group of setae; dactyl stout, with minute posterior marginal setules,unguis not overlapping palm. Gnathopod 2, basis and ischium each with strong, overlapping, hydrodynamic lobes; merus weakly extended posterodistally; carpal lobe minute; propod subovate, anterior margin with 2 proximal spines, lower margin with a few minute setae, palm oblique, slightly convex, shorter than posterior margin; dactyl regular.

Peraeopods 3-4, segment 5 regular; segment 6, posterior margin with 3 -4 uniformly weak spines; dactyl relatively slender. Peraeopods 5-7, basis variously broadened, hind margins crenulate, rounded, with weak notch and surge seta; segment 4 regular, not broadened, hind corners with cluster of 3-4 simple spines; segment 5 regular; segment 6 slender with 4-5 weak anterior marginal spines, clasping (locking) spine weak.

Epimeral plates 1-3, hind corners acuminate. Pleopods 1-3 regular. Uropod 1, peduncle with 3-4 outer marginal spines; distolateral spine stout, ~1/3 length of outer ramus; ramus with 4-5 marginal and weak apical spines. Uropod 2, rami unequal, each with 3-4 marginal spines, Uropod 3, peduncle distinctly longer than short ramus, with 1-2 short posterodistal spines; ramus blunt, with 3-4 short apical spines.

Telson, narrowly triangular, lateral margins bare.

Female ov (7.0 mm.): Gnathopod 1, hydrodynamic lobe on basis weak, rounded, lacking on ischium; carpal lobe short, broad, with ~10 marginal comb spines, anterodistal setae numerous; propod short subrectangular, palm short, oblique; dactyl slightly overlapping paired palmar spines. Gnathopod 2 similar to gnathopod 1 but hydrodynamic lobe of basis slightly larger; propod slightly longer, with 2-3 groups of posterior marginal setae; dactyl not overlapping palm.

Brood plate (gnathopod 2) broadly sub-triangular, distally sharply rounded, margins with ~100 hooked setae of medium length (~1/2 brood plate width). Preamplexing notch medium, sharply incised; unguisial groove narrow, short, nearly straight;peraeonal posterodistal lobe broad, sharply rounding anteriorly.

Etymology: The authors are pleased to name this species in honour of the late Norma E. Jarrett, Ottawa, in recognition of her dedicated work on the systematics of amphipods of the North American Pacific coast.

Distributional Ecology: Southeastern Alaska and northern British Columnia to Washington State and Oregon. Dominant among seaweed at the low water level.

Remarks: *P. jarrettae* is a member of the *seticornis* group, with short setae on the flagellum of antenna 1, and setal brushes on the proximal flagellar segments of antenna 2

P. (Boreohyale) seticornis n. sp.
(Fig. 31)

Hyale seticornis Bousfield, 1981: 80 (nomen nudum)
Protohyale seticornis Bousfield 2001a:104.

Material Examined: ~805 specimens in 107 lots, SE Alaska to Oregon and Central California. ELB Station references: Bousfield (1958, 1963, 1968); Bousfield & McAllister (1962); Bousfield & Jarrett (1981).

ALASKA
Southeastern Alaska: ELB Stns, 1961: A6 (20 incl. ♂, ♀ ov), A16 (1), A18 (4), A19 (5), A20 (2), A22 (7), A23 (2), A57 (15), A75 (2), A80 (3), A121 (13), A129 (8), A147 (10), A159 (1), A164 (84), A168 (5), A171 (15).
ELB Stns, 1980: S11B1 (2), S11B2 (3), S19B1 (1).

BRITISH COLUMBIA
Queen Charlotte Islands: ELB Stns, 1957: E14a (15); H2 (1), H14a (1); W1 (1), W8 (4), W11 (3), W12 (7).
North Central Coast: ELB Stns., 1964: H1 (2), H8 (1), H10 (11), H12 (11), H23 (6), H32 (1), H35 (6), H39 (48), H50 (14), H57 (3), H58 (2).
South Central Coast: ELB Stn, 1955: M2 (26)
Northern Vancouver Island: ELB Stns, 1959: N1 (5), N4 (1), N6 (18), N16 (3); O1 (20), O5 (30), O7b (2), O12 (2), O15 (22), O17 (1); V5 (20).
Southern Vancouver Island: ELB Stns., 1955: F4 (1), F5 (6), F5b (4). F7 (8); P4 (36), P6a (♂,♀) P7 (8).
ELB Stns 1964: H40 (1), H41 (1), H44 (1).
ELB Stns., 1970: P702 (7), P703 (7), P710 (1), P711 (19), P712, Haines I., Trevor Channel, Berkley Sound (48°47'N. 125°25'W), kelp, eelgrass, bedrock, boulders, LW, July 21 - ♂ (6.5 mm) **Holotype** (slide mount), CMNC 1983-1535; ♀ ov (5.5 mm) **Allotype** (slide mount), CMNC 1983-1536; 2 spmns **Paratypes,** CMNC 1983-1537; P714 (5), P715 (1), P719 (25).
ELB Stns, 1975: P5a (3), P20 (15), P29 (1), P32 (1).
ELB Stns, 1976: B3 (4), B5 (2), B13 (6), B28 (5).
ELB Stns, 1977: B19b (11).

Additional British Columbia material, CMN collections: Ucluelet, C. S. Young & W. Spreadborough colls., summer, 1909 - 6 spms; Queen Charlotte Islands, Stewart Houston coll., 1955 - 3 spms; Gonzales Pt., G. C. Carl coll., 1941 - 3 spms; G. C. Carl Stn 2242-5, 1955 - 35 spms; Glacier Bay, R. K. Lee, 1971 - 12 spms; Botany Bay, R. K. Lee coll., 1971 - 1 spm; Cable Beach, Mills peninsula, V. I., Stewart Houston coll., - 1 spm; D. Kittle Stns 319, 342, 1972 - 2 ♂♂, 5 ♀♀; Quisitis Pt., Wickaninnish Bay, C. L. Lobban coll.,

1971- 4 ♀♀, 1 im; Haines I., Vancouver I., L. Daniels coll., Aug. 8, 1976 - 1 ♂, 1 ♀ (slide mounts); Descansa Bay, Gabriola I., R. M. O'Clair Stn. 760025, 1976 - 1 ♂; Barnard Hbr., Princess Royal I., 1971 - 1 ♂ (978-263).

Barkley Sound, P. Lambert coll., 1973, CMN collections: Wouwer I. - 30 ♂♂, 33 ♀♀ ov, 3 im, + 12 ♂♂, 24 ♀♀, 6 im; Pigot Islets - 29 ♂♂, 27 ♀♀, 6 im; Camblain I. rock - 8 ♂♂, 4 ♀♀, 2 im; southeastern Howell Id. - 1 ♀♀.

WASH-OREGON

ELB Stns, July-Aug., 1966: W2 (2), W22 (1), W24 (1), W34 (7), W35 (10), W36 (1), W40 (1), W50 (4), W57 (7), W58 (4), W60 (1), W61 (6), W63 (9).

Eagle Cove, San Juan I., R. M. O'Clair Stn 740011, 1974 - 3 spms; Limestone Pt., San Juan, R. I. Smith coll., 1955 - 1 spm.

CALIFORNIA

Albion Cove Rocks, Mendocino Co. (39°14'12"N, 123° 45'W), associated with *Ammothalla tuberculata*, 20m., T. Chess coll., June 29, 1978 - 1 spm.; Ibid. - 2 spms. (ident. K. E. Conlan), CMN Acc. No. IZ1986-057.

Diagnosis:. Male (9.0 mm.): Eyes medium, subcircular. Antenna 1, peduncular segments strong, 2 distinctly larger than 3; flagellum with 16-18 segments, each bearing 2-3 medium strong setae and 2 aesthetascs. Antenna 2 medium short, less than twice length of antenna 1; flagellum with 30-33 segments, setal brushes conspicuous on proximal segments.

Upper and lower lips lightly pilose apically. Mandible, left lacinia 5-dentate; spine row with 2-3 accessory blades. Maxilla 1, palp elongate, tip reaching about 1/3 length of apical spine teeth of outer plate. Maxilla 2, inner plate with inner row of 8-9 pectinate setae. Maxilliped palp medium sout; dactyl as long as segment 3, unguis medium.

Coxae 1-4 large, posterior marginal cusp lacking, posterior marginal shelf very weak on coxae 1-3, lower margins nearly straight. Coxa 5 aequilobate. Coxal gills sac-like, largest on peraeopods 4 and 5.

Gnathopod 1, hydrodynamic lobe medium and broadly rounded on basis; virtually lacking on ischium; carpus lobe medium broad, with ~15 marginal comb setae; propod short, subovate, with 2-3 anterodistal spines, palm very short, oblique, posterior angle defined by a pair of slightly separated short spines, distal portion of posterior margin with single linearly spread cluster of setae; dactyl stout, with minute posterior marginal setules, unguis not overlapping palm. Gnathopod 2, basis and ischium each with strong, overlapping, hydrodynamic lobes; merus weakly extended post-erodistally; propod subovate, anterior margin with 2-3 proximal spines, lower margin with a few minute setae, palm oblique, nearly straight, about equal to posterior margin; dactyl regular.

Peraeopods 3-4, segment 5 regular, shorter on peraeopod 4, regular; segment 6, posterior margin with 4-5 spines strengthening distally; dactyl regular. Peraeopods 5-7, basis variously broad, hind margins slightly crenulate, rounded, with distinct notch and surge seta; segment 4 slightly broadened, hind corners with cluster of 3-4 simple spines; segment 5 stout; segment 6 stout, with 4-5 medium anterior marginal spines, clasping (locking) spine small.

Epimeral plates 1-3, hind corners weakly acuminate. Pleopods 1-3 regular. Uropod 1, peduncle with 2-3 outer marginal spines; distolateral spine regular, outer ramus having 3-4 marginal and a few weak apical spines. Uropod 2 relatively large, rami unequal, each with 3 marginal spines, Uropod 3, peduncle distinctly longer than short blunt ramus, with 3 short posterodistal spines; ramus with 4-5 short apical spines.

Telson lobes subtriangular, curved, lateral margins bare.

Female ov (7.0 mm.): Gnathopod 1, hydrodynamic lobe on basis weak, sharply rounded, lacking on ischium; carpal lobe short, broad, with ~10 marginal comb spines, anterodistal setae few; propod short subrectangular, palm short, oblique; dactyl slightly overlapping paired palmar spines, posterior margin with nearly continuous row of short setae. Gnathopod 2 similar to gnathopod 1 but hydrodynamic lobe of basis slightly larger; carpal lobe narrow; propod slightly longer and deeper, with 2 separated groups of posterior marginal setae; dactyl not overlapping palm.

Brood plate (gnathopod 2) broadly sub-triangular, distally more braodly rounded, margins with ~90 hooked setae of medium length (<1/2 brood plate width). Preamplexing notch medium, sharply incised; unguisial groove narrow, very short, straight;peraeonal posterodistal lobe broad, evenly rounded anteriorly.

Etymology. From the Latin "*seta*" and "*cornu*" (horn), with reference to the posteriorly strongly setose peduncular segments of antenna 1.

Distributional Ecology: *Protohyale seticornis* is a common intertidal and subtidal species of rocky shores, of the northwestern Pacific region, from southeastern Alaska to central California.

Remarks: The *seticornis* group is characterized by a setose flagellum of antenna 1, and setal brushes on the proximal flagellar segments of antenna 2.

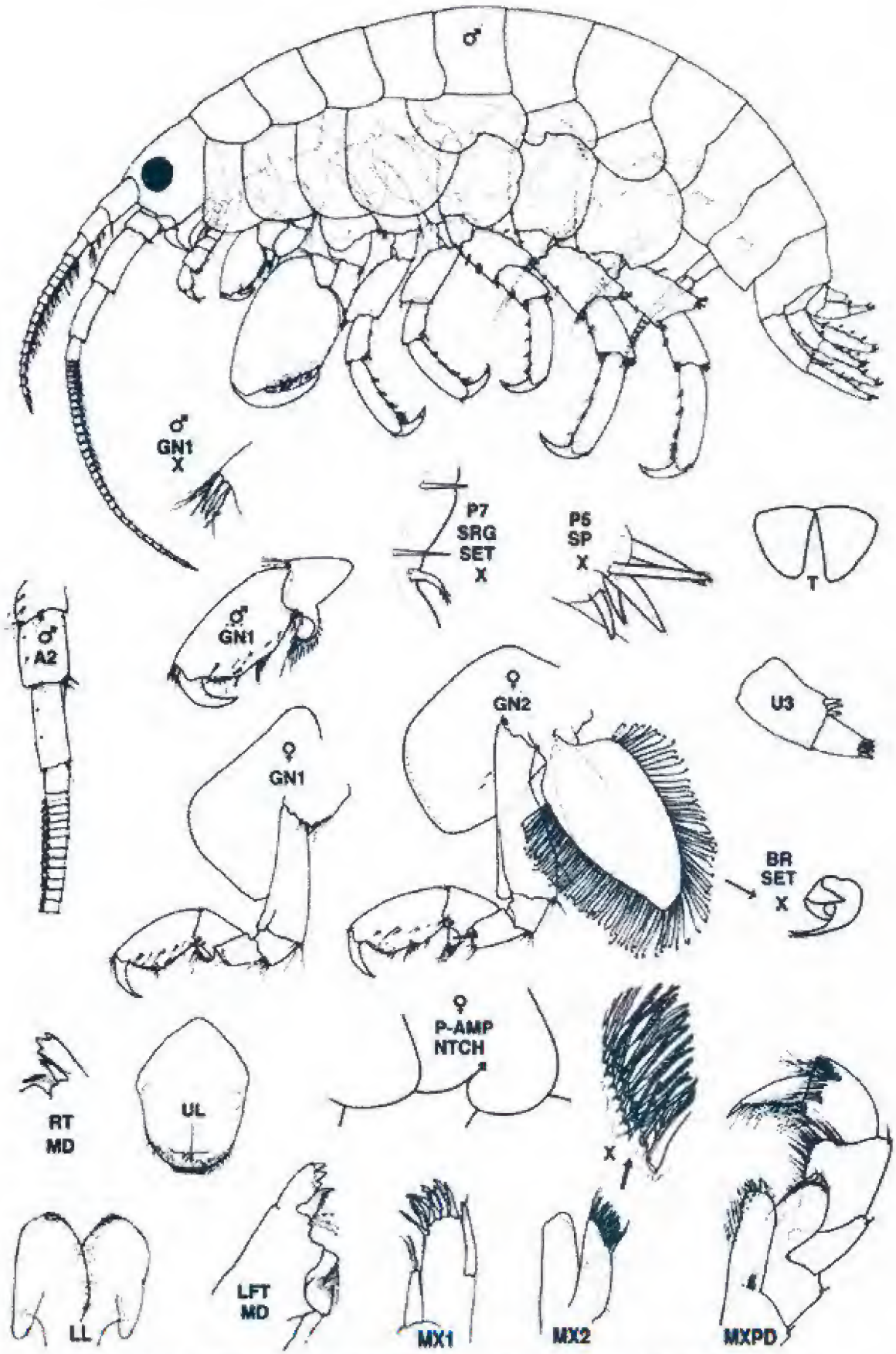

Fig. 31. *P. (Boreohyale) seticornis* n. sp. Male (6.5 mm); female ov (5.5 mm). ELB Stn P712, David I.,Barkley Sound, B. C.

P. (Boreohyale) seticornis is close to *P. (B.) hiwatarii* (p. 76) but is distinguished from the latter in the following features: eye size is medium to small (vs. large); antenna 1: strongly setose; antenna 2: peduncular segments and flagellum have setal brushes on inner margin anteriorly (vs. posterior margin), and the flagella segment number 23 (vs. 15); uropod 3, peduncle with 4 apicodorsal spines (vs. 2).

P. seticornis also resembles *P. jarrettae*, but differs from it by characters of the key (p. 64) and the following features: antenna 2, peduncular segments and flagellum have setal brushes on inner margin anteriorly (vs. setal brushes on anterior and posterior margins), number of flagellar segments is 23 (vs. 14);and maxilliped, dactyl of palp is slightly longer than segment 3 (vs.equal to segment 3).

The species name *seticornis* was not included within genus *Hyale* in Barnard & Karaman (1991), but is here made taxonomically available within the new genus name *Protohyale*.

Protohyale (Boreohyale) oculata n. sp.

(Fig. 32)

Hyale oculata Bousfield 2001a: 104 (nomen nudum)

Material Examined:

BRITISH COLUMBIA

Southern Vancouver Island: ELB Stn P715, Gonzales Bay, Victoria (48° 25'N, 123°20'W), kelp over bedrock, LW, July 29, 1970 - ♂ (7.5 mm) **Holotype** (slide mount) CMNC 1983-1508.

WASH-OREGON

Eagle Cove, San Juan I., WA, R. M. O'Clair coll., June 21, 1974 - 1 ♀ ov (5.3 mm) **Allotype** (slide mount).

Diagnosis:. Male (7.5 mm.): Eyes large, broadly almond-shaped. Antenna 1 short, peduncular segments strong; flagellum short, with 6-8 lightly setose segments. Antenna 2 short, scarcely twice length of antenna 1; flagellum short, with about 15 weakly setose segments,

Upper and lower lips regular. Mandible, left lacinia 5-dentate; spine row with 2-3 accessory blades. Maxilla 1, palp relatively short, tip reaching little beyond base of apical spine teeth of outer plate. Maxilla 2, inner plate with inner row of 8-9 pectinate setae. Maxilliped palp relatively slender; dactyl as long as segment 3, setose medially, unguis slender.

Coxae 1-4 large, strongly rounded below, posterior marginal cusp lacking, posterior marginal shelf vestigial. Coxa 5 slightly posterolobate. Coxal gills platelike, largest on peraeopods 4 and 5.

Gnathopod 1, hydrodynamic lobe virtually lacking on basis and ischium; carpus lobe narrow, with ~12 marginal comb setae; propod relatively large, subovate, with 3 anterodistal spines, palm very short, oblique, posterior angle defined by a pair of short spines, distal portion of posterior margin slightly convex, with linear row of 7-8 setae; dactyl stout, with minute posterior marginal setules, slightly overlapping palm. Gnathopod 2, basis and ischium each with strong, overlapping, hydrodynamic lobes; merus weakly extended posterodistally; propod subquadrate, anterior margin with 2 proximal spines, lower margin virtually bare, palm oblique, slightly convex, slightly shorter than posterior margin; dactyl regular.

Peraeopods 3-4 regular; segment 6, posterior margin with 4-5 spines strengthening distally; dactyl relatively short. Peraeopods 5-7, basis broadly rounded, hind margins crenulated, with distinct notch and surge seta; segment 4 slightly broadened distally, hind corners each with cluster of 3-4 simple spines; segment 5 shorter than 4; segment 6 regular, with 3-4 medium anterior marginal spines, clasping (locking) spine medium.

Epimeral plates 2-3, hind corners distinctly acuminate. Pleopods 1-3 regular. Uropod 1, peduncle with 2 outer marginal spines, distolateral spine regular, outer ramus with 2 distal marginal and a few weak apical spines. Uropod 2 relatively large; rami unequal, stout, tapering, longer than peduncle, each with 2 marginal spines, Uropod 3, peduncle stout, sith single posterodistal spine;ramus short, tapering subacute apex with a few very short spines.

Telson lobes longer than wide, apically subacute.

Female (5.3 mm): Character states similar to those of *P. (B.) oclairi* (p. 71).

Etymology. The specific name refers relatively large darkly pigmented eye, that occupies about 1/4 lateral area of the head.

Distributional Ecology: Known only from the Juan de Fuca and Puget Sound region of southern British Columbia and northern Washington state; among algae at the LW level of rocky shores.

Remarks: *Protohyale oculata* is close to *P. oclairi* (p. 74) among the primitive North Pacific subgroup. It is distinguished from *oclairi* by its relative short antenna 2, shorter dactyl of the maxilliped palp, short ramus of uropod 3, and much larger eye.

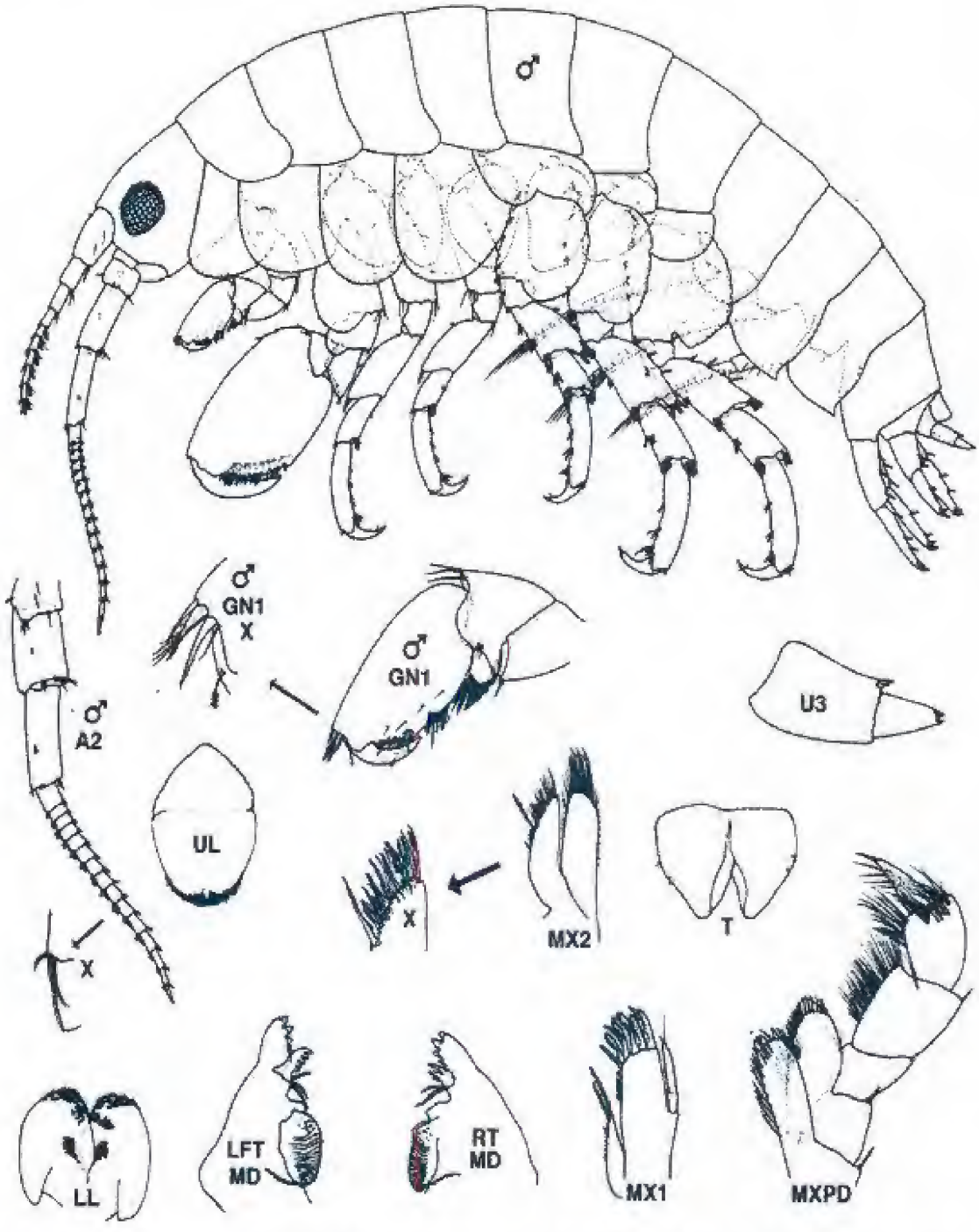

Fig. 32. ***P. (Boreohyale) oculata*** **n. sp.** Male (7.5 mm). ELB Stn P715, Gonzales Bay, Victoria, B. C.

Protohyale (Boreohyale) oclairi n. sp.

(Fig. 33)

Hyale oclairi Bousfield, 1981 (unpubl. MS name)
Protohyale oclairi Bousfield 2001a: 104 (nomen nudum).

Material Examined: ~175 specimens at 24 stations, from SE Alaska to Washington State. ELB station references: Bousfield (1958, 1963, 1968), Bousfield & McAllister (1962); Bousfield & Jarrett (1981).

ALASKA
S.E. Alaska. ELB Stns., 1961: A6, Prince of Wales I., east of Pt. Marsh - 2 males.

BRITISH COLUMBIA
Queen Charlotte Islands: ELB Stn, 1957: W11 (1).
North Central Coast: ELB Stn, 1964: H53 (1).
South Central Coast: ELB Stn, 1955: M2 (1).
Northern Vancouver Island: ELB Stn, 1959: N16 (1).
Southern Vancouver Island: ELB Stns, 1955: F3 (2), F4a (1), F5 (13); P5 (2), P7 (121).

ELB Stn, 1970: P715 (1).
ELB Stn, 1975: P5c (2).

WASH-OREGON
ELB Stns. July-Aug., 1966: W34 (2), W60 (10). W66 (3).
Eagle Cove, San Juan I., WA (48 °27'42"N, 123°01'54"W), R. M. O'Clair coll, June 21, 1974 - ♂ (7.1 mm) **Hototype** (slide mount) CMNC 1983-1514; ♀ ov (5.3 mm) **Allotype** (slide mount), CMNC 1983-1515; 2 ♂♂, 6 ♀♀, 12 im **Paratypes**, CMNC 1983-1516.
Additional Material (CMN collections)
British Columbia: Victoria Hbr., R. Long coll, 1977 - 3 specimens; Glacier Pt., Knight Inlet, R. K. Lee, 1972 - 5 specimens; Banks I., Broken Group, Barkley Sound, C. L. Lobban coll. - 1 ♀; Gibraltar I., Barkley Sound, P. Lambert coll. 1973 - 1 ♂; B. Westerberg, #33, 10-mile pt, Victoria, 1964 - 1♂.

Diagnosis: Male (7. 1 mm.). Eye relatively small, subovate. Antenna 1 short, peduncular segments strong; flagellum medium, with ~12 posteriorly setose segments. Antenna 2 medium, about twice length of antenna 1; peduncular segments 4 & 5 strong; flagellum with about 30 short-setose segments,

Upper and lower lips regular. Mandible, left lacinia 5-dentate; spine row with 2-3 accessory blades. Maxilla 1, palp relatively short, tip reaching little beyond base of apical spine teeth of outer plate. Maxilla 2, inner plate with inner row of 8-9 pectinate setae. Maxilliped palp relatively slender; dactyl as long as segment 3, setose distally, unguis slender.

Coxae 1-3 medium, rounded below,posterior marginal cusp lacking, posterior marginal shelf shallow. Coxa 4 broadest. Coxa 5 slightly anterolobate. Coxal gills slender, saclike, broadest on peraeopod 4.

Gnathopod 1, hydrodynamic lobe virtually lacking on basis and ischium; carpal lobe medium, short, with 9-10 marginal comb setae; propod slender, elongate-ovate, with 2 anterodistal spines, palm very short, oblique, posterior angle defined by a pair of separated spines, distal portion of posterior margin with a small proximal and distal larger cluster of 6-7setae; dactyl stout, with minute posterior marginal setules, unguis overlapping palm. Gnathopod 2, basis and ischium each with broadly rounded, overlapping, hydrodynamic lobes; merus weakly extended posterodistally; carpal lobe vestigial; propod deeply subovate, anterior margin with 2 proximal spines, lower margin bare, palm short, oblique, lined with spines, convex near hinge; dactyl regular.

Peraeopods 3-4 relatively slender; segment 6, posterior margin with 4 spines strengthening distally; dactyl relatively short. Peraeopods 5-7, basis broadly rounded, hind margins weakly crenulated, each with distinct notch and surge seta; segment 4 slightly broadened distally, hind corners each with cluster of 4-5 prominent simple spines; segment 5 slightly shorter than 4; segment 6 regular, with 4-5 medium anterior marginal spines, clasping (locking) spine medium.

Epimeral plates 2-3, hind corners acuminate. Pleopods regular. Uropod 1, peduncle with 3-4 outer marginal spines, distolateral spine short; outer ramus with 2 distal marginal and a few weak apical spines. Uropod 2, rami unequal, tapering, longer than peduncle, each with 2 marginal spines. Uropod 3, peduncle stout, with pair of posterodistal spines; ramus slightly shorter than peduncle, tapering distally, apex blunt, armed with 4-5 short spines.

Telson lobes subacute, weakly fused basally.

Female ov (5.3 mm.): Gnathopod 1, basis and ischium lacking hydrodymanic lobes; carpal lobe medium, with 10-12 marginal comb spines, anterodistal setae few; propod subrectangular, slightly arched, palm short, oblique; dactyl slightly overlapping paired palmar spines, posterior margin with cluster of short setae. Gnathopod 2 similar to but slightly larger than gnathopod 1 and basis with small hydrodynamic lobe; carpal lobe narrow; propod, posterior marginal small proximal and larger distal group of short setae; dactyl not overlapping palm.

Brood plate of gnathopod 2 relatively short, broadly rounded distally margins with about 90 relatively long hooked setae (length >1/2 width of brood plate). Preamplexing notch with deep oblique unguisial groove,

Etymology. The species is named in honour of Dr. Charles E. O'Clair, in recognition of his development of knowledge of coastal marine faunas of the Aleutian Islands and southeastern Alaska.

Distributional Ecology: Among algae at the lower intertidal level, southeastern Alaska to Oregon.

Remarks: *P. (Boreohyale) oclairi* is a relatively uncommon species of the primitive cool-temperate subgroup of *Protohyale*. Superficially similar to *P. (B.) pumila* Hiwatari & Kajahari, 1981a (p. 80), *P. (B.) oclairi* is distinguished from it in the following features: size small to medium (vs. medium large); antenna 2, peduncular segments and flagellum with setal brushes anteriorly on inner margin (vs. posterior margin); gnathopod 1 (♂), propod subrectangular (vs. deep ly broadened distally); and brood plate (gnathopod 2) narrowing distally (vs. broadly subovate and rounded

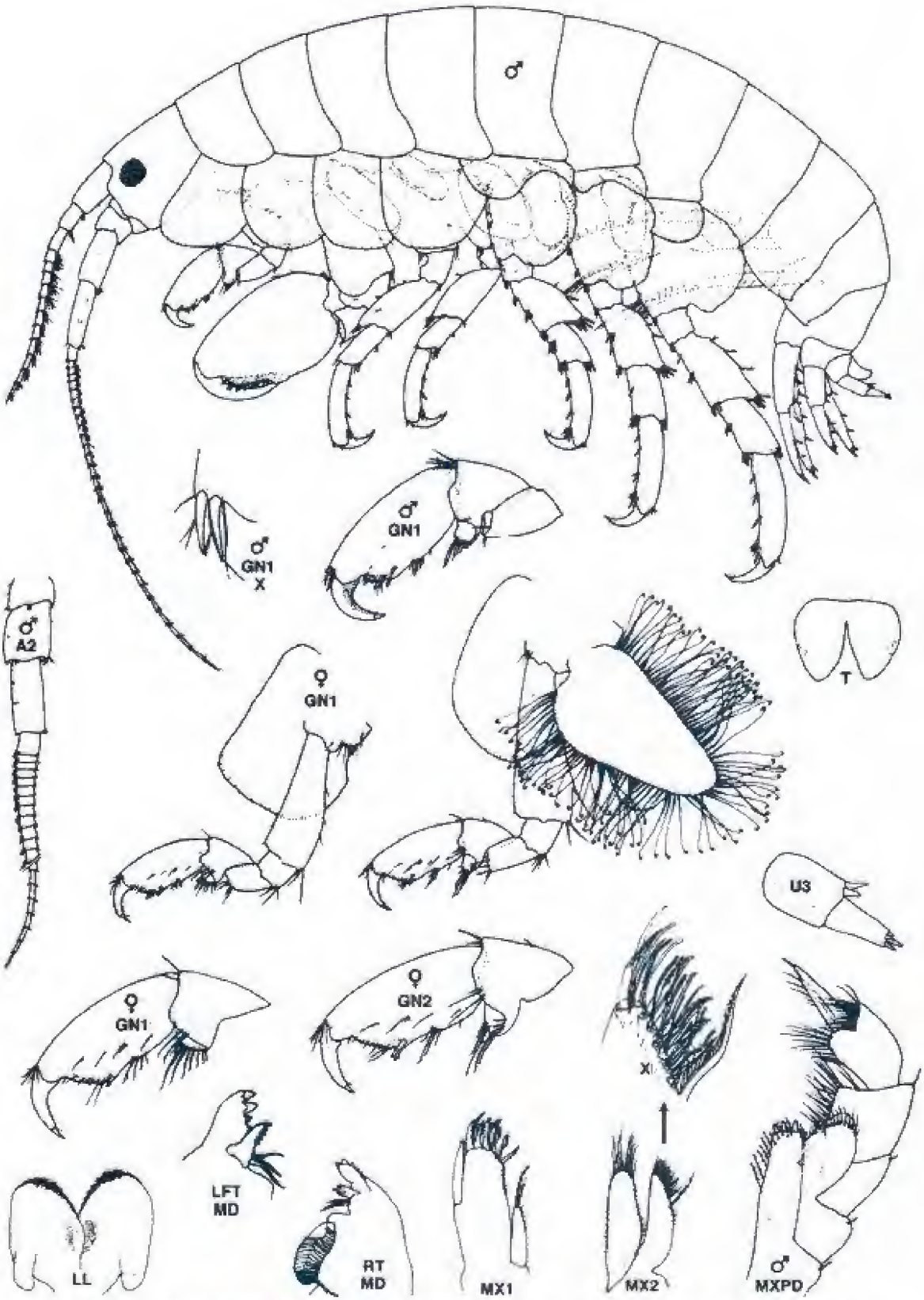

Fig. 33. ***P. (Boreohyale) oclairi* n. sp.** Male (7.1 mm); female ov (5.3 mm). Eagle Cove, San Juan I., WA

distally). Eastern North Pacific species of *Boreohyale* appear not closely related to those of the western North Pacific.

Protohyale Boreohyale) hiwatarii n. sp.
(Fig. 34)

Hyale spinosa Bousfield, 1981 (unpubl. MS name)
Protohyale spinosa Bousfield, 2001a: 104 (nomen nudum).

Material Examined 6 specimens at 3 stations, southeastern Alaska to northern Washington state.

ALASKA
Southeastern Alaska: ELB Stn, 1961: A59, Thistle Cove, Dixon Harbor, greenling stomach content - 1 ♀ ov.

BRITISH COLUMBIA
Southern Vancouver Island: Saturna I., from floating kelp fronds, I. McT Cowan coll., 1954 - 1 ♂ (slide mount).

WASH-OREGON
Friday Harbor(48°32'N, 123°02'W), kelp at LW, ELB coll., Aug. 24, 1959 - ♂ (11 mm) **Holotype** (slide mount), CMNC 1983-1506; ♀ ov (9.0 mm)**Allotype** (slide mount), CMNC 1983-1505; 24 spms. **Paratypes**, CMNC 1983-1507.

Diagnosis: Male (11.0 mm): Eyes medium, broadly almond-shaped. Antenna 1, peduncular segment 2 distinctly larger than segment 3; flagellum with ~16 segments, each bearing 2 aesthetascs and a few short setae. Antenna 2 medium, about twice length of antenna 1; flagellum with 30-35 segments,short setal brushes on proximal segments.

Upper and lower lips lightly pilose apically. Mandible, left lacinia 5-dentate, spine row with 2-3 accessory blades. Maxilla 1, palp elongate, tip reaching about 1/3 length of apical spine teeth of outer plate. Maxilla 2, inner plate with inner row of 8-9 pectinate setae. Maxilliped palp slender; dactyl as long as segment 3, inner margin with row of long setae, unguis short.

Coxae 1-4 large, lower margins rounded; posterior marginal cusp lacking, posterior marginal shelf very weak on coxae 1-3. Coxa 5 aequilobate. Coxal gills large, laminar, largest on peraeopods 4 & 5.

Gnathopod 1, hydrodynamic lobe of basis weak, shallow, virtually lacking on ischium; carpal lobe medium broad, with 10-12 marginal comb setae; propod short convexly subrectangular, with 1 stout and 1 slender anterodistal spine, palm short, oblique,posterodistal angle with pair of slightly displaced spines, distal portion of posterior margin with broken row of setae; dactyl stout, with minute posterior marginal setules, unguis slightly overlapping palm. Gnathopod 2, basis and ischium each with broadly rounded overlapping, hydrodynamic lobes; merus acutely extended posterodistally; propod deeply subovate, anterior margin with 2 proximal spines, lower margin distally with small seta, palm short, oblique, nearly straight, lined with stout spines; dactyl regular.

Peraeopods 3-4, segment 5 regular, shorter on peraeopod 4; segment 6, posterior margin with 4-5 spines strengthening distally; dactyl shorter than in peraeopods 5-7. Peraeopods 5-7 stout, basis relatively narrow, hind margins slightly crenulate; segment 4 somewhat broadened, hind corners with cluster of 3-4 simple spines; segment 5 short; segment 6 stout, with 4-5 pairs of anterior marginal spines, clasping (locking) spine medium strong.

Epimeral plates 2-3, hind corners acuminate. Pleopods regular. Uropod 1, peduncle with 4-5 outer marginal spines; distolateral spine short, outer ramus having 3-4 marginal and a few weak apical spines. Uropod 2, rami unequal, longer than short peduncle, each with 2-3 marginal spines. Uropod 3, peduncle short, stout,with 3 short posterodistal spines; ramus short, blunt, with 3-4 short apical spines.

Telson lobes subtriangular, little longer than wide, curved lateral margins bare.

Female ov (8.0 mm.): Gnathopod 1, carpal lobe small, with 8 marginal comb spines, anterodistal setae few; propod subrectangular; palm short, oblique; dactyl slightly overlapping paired palmar spines, posterior margin proximally with nearly continuous row of distally lengthening setae. Gnathopod 2 very similar to gnathopod 1 but hydrodymanic lobe of basis slightly larger; carpal lobe narrow; propod slightly longer and deeper, with single small group of posterior marginal setae; dactyl not overlapping palm.

Brood plate (gnathopod 2) short, very broad, distally rounded, margins with ~80 relatively long hooked setae (length >1/2 brood plate width). Preamplexing notch shallow, with deep oblique unguisial grove; posterodistal lobe of peraeon 2 shallow, anterior margin sharply rounded.

Etymology. The patronym recognizes Dr. Hiwatari's significant and continuing contributions to knowledge of amphipod systematics in the western North Pacific region.

Distributional Ecology: A relatively rare species, taken only among seaweed in the lower intertidal zone, mainly in the southern part of the Strait of Georgia.

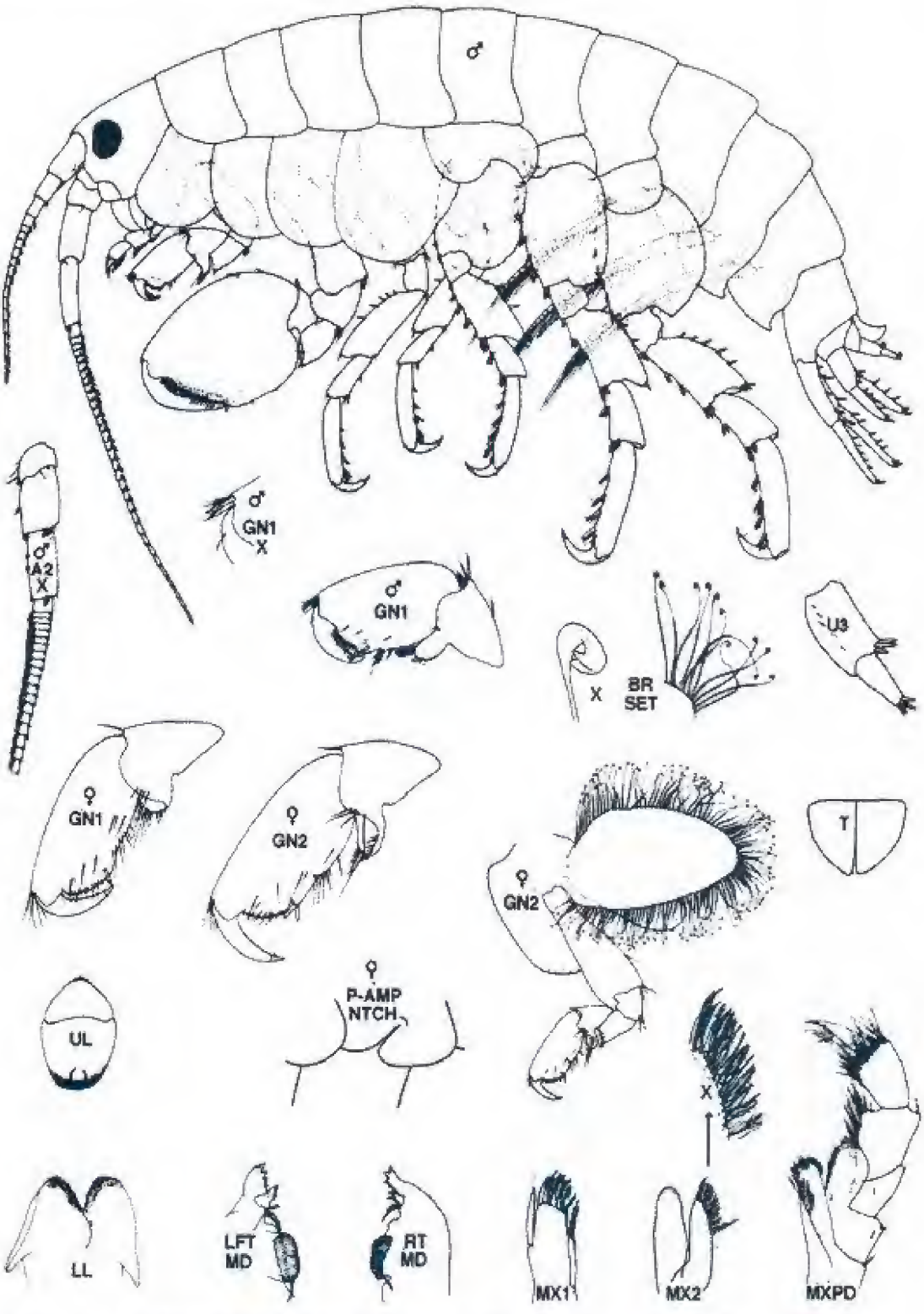

Fig. 34. ***P. (Boreohyale) hiwatarii* n. sp.** Male (11.0 mm); female ov. (9.0 mm). Friday Harbor, WA, USA

Remarks: *P. (Boreohyale) hiwatarii* is distinguished from *P. (B.) pumila* (Hiwatari & Kajihara, 1981a) in the following features: eyes medium to small (vs. large), antenna 2 peduncular segments and flagellum have setal brushes on inner anterior margin (vs. posterior margin), and the number of flagellar segments is 23 (vs. 15). In *P. (B. pumila)*, the propod of gnathopod 1(♂) is much deeper, with a posterodistal protrusion.

***Protohyale (Boreohyale) neorionensis* n. sp.**
(Fig. 35)

Hyale brevicornis Bousfield, 1981 (unpubl. MS)

Material Examined:
BRITISH COLUMBIA
Southern Vancouver Island: ELB Stn. 1955: F5, Victoria Dallas breakwater (48°25'N, 123°23'W), LW, Aug. 20 - ♂ (7.5 mm) **Holotype** (slide mount), 1983-1517; ♀ ov (5.0 mm) **Allotype** (slide mount), CMNC 1983-1518.

Diagnosis. Male (7.5 mm.): Eyes medium, broadly almond-shaped. Antenna 1, peduncular segment 3 not exceeding distal end of peduncle 4 of antenna 2; flagellum 12- segmented each bearing 2 aesthetascs and a few short setae. Antenna 2 relatively short, about twice length of antenna 1; inner margin of peduncular segments 4, 5 and proximal 10 articles of 23-segmented flagellum bearing short setae anteromedially.

Upper and lower lips regular. Mandible, left lacinia 5 1/2-dentate, with 2-3 accessory blades. Maxilla 1, palp slender, reaching just beyond base of apical spine teeth on outer plate. Maxilla 2 regular; inner margin of inner plate with pectinate setae. Maxilliped palp slender; dactyl with row of relatively long inner distal setae, length equal to segment 3, unguis short.

Coxae 1-3 , posterior marginal shelf shallow, cusp lacking, lower margins shallowly convex, not crenulated. Coxa 4 with simple posteroproximal excavation, median cusp slight. Coxal gills 2-6 large, plate-like largest on peraeopod 5

Gnathopod 1, hydrodynamic lobe of basis medium, sharply rounded; merus slightly produced; carpal lobe short bearing 10-12 comb ; propod short subovate, with single stout anterodistal spine, palm short, oblique, posterior angle defined by a pair of short spines, distal portion of posterior margin with two small clusters of short setae; dactyl stout, with minute posterior marginal setules, unguis not overlapping palm. Gnathopod 2, basis and ischium each with broadly rounded overlapping, hydrodynamic lobes; merus acutely extended posterodistally; propod deeply subovate, anterior margin with 2 proximal spines, lower margin distally with small seta, palm short, oblique, nearly straight; dactyl regular.

Peraeopods 3-4, segment 5 regular, shorter on peraeopod 4; segment 6, posterior margin with 4-5 spines strengthening distally; dactyl shorter than in peraeopods 5-7. Peraeopods 5-7 stout, basis relatively narrow, hind margins slightly crenulate; segment 4 somewhat broadened, hind corners with cluster of 3-4 simple spines; segment 5 short; segment 6 stout, with 4-5 pairs of anterior marginal spines, clasping (locking) spine medium strong.

Epimeral plates 2-3, hind corners acuminate. Pleopods regular. Uropod 1, peduncle with 4-5 outer marginal spines; distolateral spine short, outer ramus having 3-4 marginal and a few weak apical spines. Uropod 2, rami unequal, longer than short peduncle, each with 2-3 marginal spines. Uropod 3, peduncle short, stout,with 2 short posterodistal spines; ramus short, blunt, with 3-4 short apical spines.

Telson lobes subtriangular, little longer than wide; curved lateral margins bare.

Female ov (5.0 mm.): Gnathopod 1, hydrodynamic lobe on basis very small; carpal lobe short, with 8 marginal comb spines, anterodistal setae few; propod subrectangular; palm short, oblique; dactyl slightly overlapping paired palmar spines, posterior margin proximally with nearly continuous row of distally lengthening setae. Gnathopod 2 similar ; merus more sharply produced; propod subrectangular, palm oblique, simple, defined by a pair of heavily striated spines, distal half of posterior margin with 2 groups of short setae; dactyl not overlapping palmar spines. Brood plate on gnathopod 2 short, very broadly subtriangular, distally somewhat sharply rounded, margins with ~80 relatively long hooked setae (length >1/2 brood plate width). Preamplexing notch sharply incised, with medium deep, slightly curved unguisial groove; lower hind lobe smoothly rounded anteriorly.

Etymology. From the Greek root name "*neorion*" meaning "harbour", with reference to the dockard inside the Victoria outer harbour breakwater where the species was initially collected.

Distributional Ecology Among seaweed of surf-exposed rocky shores, southern Vancouver I., B. C.

Remarks: *Protohyale neorionensis* is a rare species, known only from the type locality in southern Vancouver Island. It is taxonomically closest to *Protohyale lamberti* but differs in its shorter, more setose antennae, more slender maxilliped palp, stouter, more spinose peraeopods, and somewhat smaller size.

Western Pacific Species of subgenus *Boreohyale*.

Although dominant in the boreal eastern North Pacific region, the subgenus *Boreohyale* is apparently represented by a few species in the western North Pacific. As Dr. Hiwatari is now in the process of revising the Hyalidae of Japan (pers. comm.), these

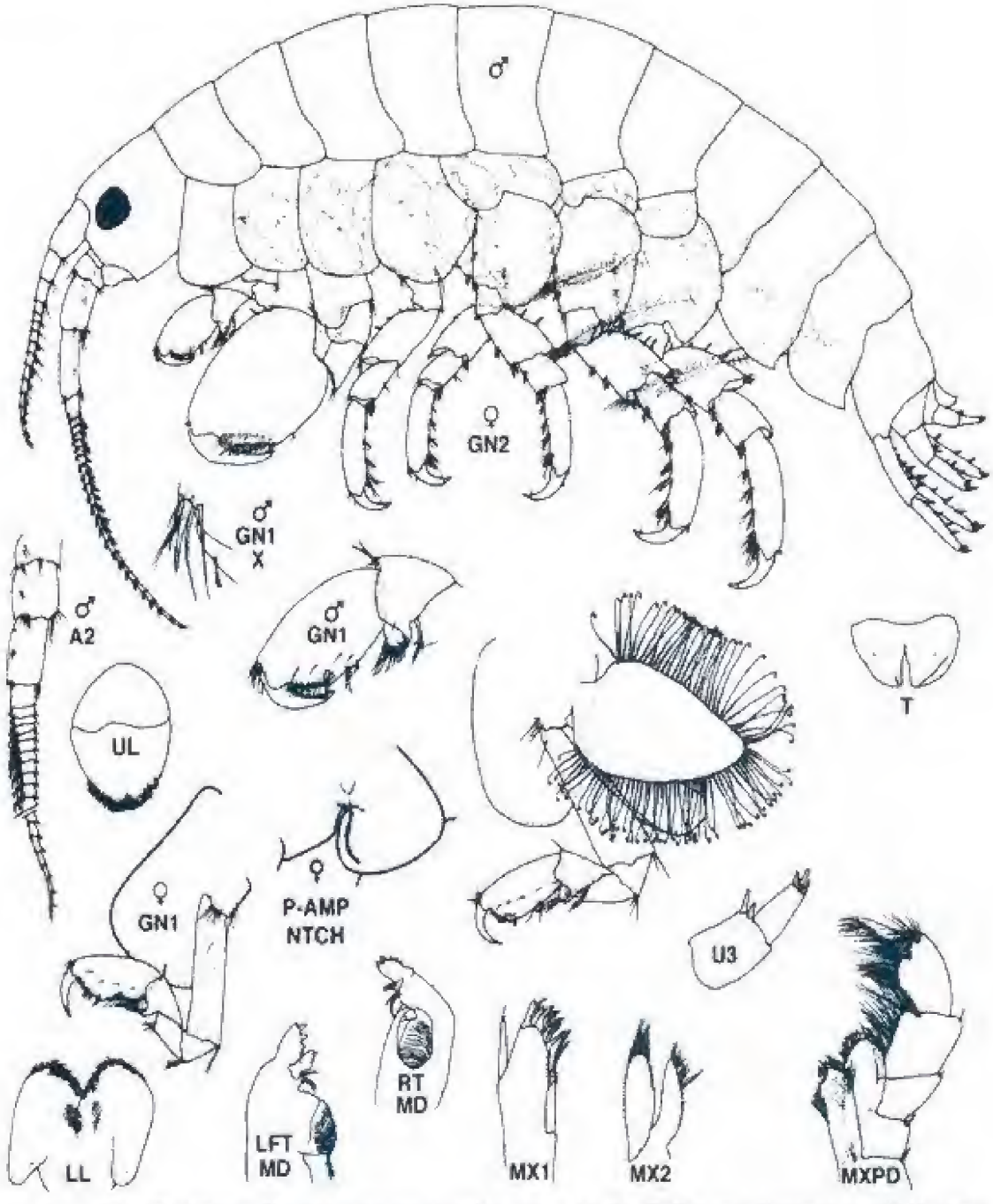

Fig. 35. ***P. (Boreohyale) neorionensis* n. sp.** Male (7.5 mm); female ov (5.0 mm) ELB Stn. F5, Victoria breakwater, B. C.

species are included here from the standpoint of systematics and biogeography of subgenus *Boreohyale* in the overall North Pacific Basin (Table III, p. 129). None of the three was recorded from Soviet shores of the Japan Sea by Derzhavin (1937) or Gurjanova (1951).

P. (Boreohyale) pumila (Hiwatari & Kajihara) (Fig. 36)

Hyale pumila Hiwatari & Kajihara, 1981a: 35, figs. 1-4;—Ishimaru 1994: 68.

Remarks: This species was described from intertidal habitats around Honshu,including Tokyo Bay, north to Hokkaido. Selected figures are reproduced here for comparison (Fig. 36). Particularly significant is the unreduced peduncular segment 2 of antenna 1, stout maxilliped palp, fully separated lobes of the telson, and lack of hyrodynamic lobes on the female gnathopods. The preamplexing notch has not been described. The elongate flagellum of antenna 2, and short deep propod of gnathopod 1 (♂) are similar to those of the *schmidti-dollfusi* complex of the European Mediterranean re-

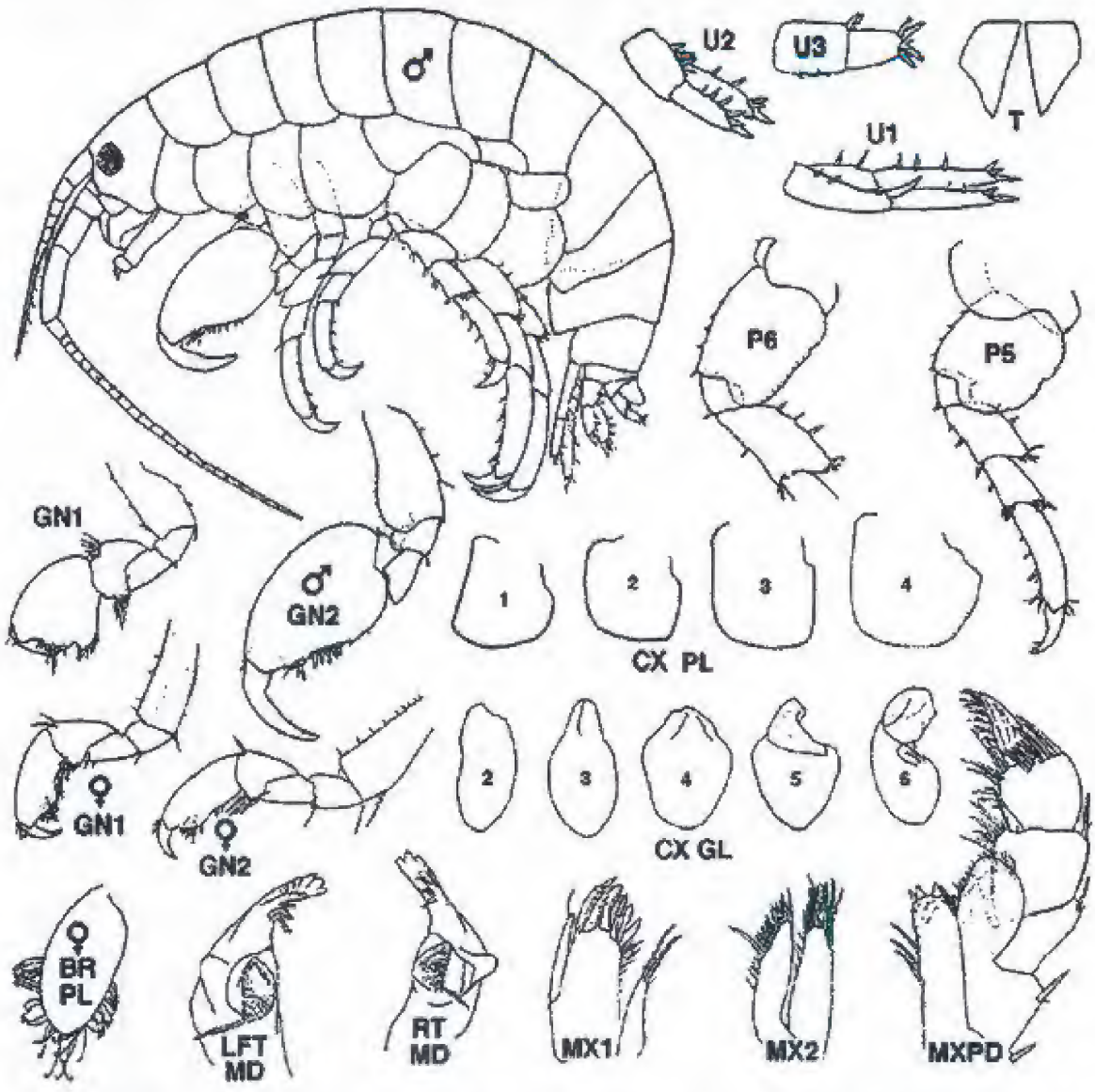

Fig. 36. *P. (Boreohyale) pumila* (Hiwatari & Kajihara, 1981). Male (11.6 mm); female ov (9.5 mm). (modifed from Hiwatari & Kajihara 1981a)

gion. The short, broad, distally rounded brood plate of gnathopod 2 (♀), the 5-dentate left lacinia, and triangular lobes of the telson are also characteristics of eastern Pacific species of *Boreohyale*.

Protohyale ?(Boreohyale) sp. 1*

Hyale schmidti Iwasa,1939: 278, pl. 17, fig. 17;—Bulycheva 1957: 96, fig. 34;—Nagata 1965: 307?
non *Hyale schmidti* (Heller, 1866).
non *Hyale pumila* Hiwatari & Kajihara 1981a: 35, figs. 1-4.

Remarks: Iwasa's original material of "*Hyale schmidti*" was recorded from Hokkaido, and subsequently from Straits of Korea (Bulycheva 1957; Nagata 1965). Bulycheva accepted Iwasa's identification and reproduced his figures. However, Hiwatari & Kajihara (1981b) included Iwasa's "*Hyale schmidti*" in the synonymy of *P. (B.) pumila* (above).

In our view, Iwasa's species is not only distinct from the European species *Hyale schmidti* (Heller, 1866) but also from *P.(B.) pumila* (above)*. Iwasa's material differs in the distally narrowing propod of gnathopod 1 (male); in the elongate and sharply rounded brood plate of gnathopod 2 (female) , in its much more slender and elongate maxilliped palp, and in the rather broader and shorter lobes of the telson. The unusually elongate and distally subacute brood plate is a character state not typical of genus *Protohyale*.

Protohyale ?(Boreohyale) sp. 2

Hyale dollfusi Bulycheva 1957:105, fig 38.
Hyale dollfusi? Iwasa 1939: 280, 18 fig. 18;—Stephensen: 1944: 69, fig. 24;—Ishimaru 1994: 68.
non: *Hyale dollfusi* Chevreux, 1911: 238, t. 16, fig. 13; —Chevreux & Fage 1925: 287, fig. 298.
non: *Hyale schmidti* Krapp-Schickel 1993:736, fig. 504.

Remarks: Bulycheva (loc. cit.) recorded and figured a hyalid species from an unspecified locality as "*Hyale dollfusi* Chevreux, 1911. However, her material differs from European material of that species, as illustrated by Chevreux & Fage (1925) and Krapp-Schickel (1993), who may have incorrectly synonymized *P. (B.) dollfusi* with *P. (B). schmidti*.

Bulycheva's species is distinguished by relatively short flagellae of antennae 1 & 2, proximally broad basis of peraeopod 6, and strongly produced hind corner of epimeral plate 3. Her species is similar to Iwasa's *P. "schmidti"* in the elongate and sharply rounded brood plate on gnathopod 2, and relatively short lobes of the telson. However, the deep form of the propod of gnathopod 1 (♂), form of the brood plate of gnathopod 2 (♀), and overall size range tend to support Bulycheva's initial decision to assign the westen Pacific material to *P. (B.) dollfusi* of the Mediterranean region.

Protohyale (Protohyale) nominate subgenus

Hyale (part) Barnard 1979 (*rubra frequens* subgroup); Barnard & Karaman 1991: 367.

Type species: *Allorchestes frequens* Stout, 1913.

Species: *Protohyale (Protohyale) affinis* (Chevreux, 1907); *?P. (P.) campbellica* (Filhol,1885) (Hurley, 1957); *P. (P.) canalina* (Barnard, 1979); *P. (P.) corallinacola* (Hirayama, 1980); *P. (P.) dollfusi* (Chevreux, 1911); *P. (P.) frequens* (Stout, 1913); *P. (P.) grimaldii* (Chevreux, 1891); *P. (P.) inermis* (Ledoyer,1978, 1979a); ***P. (P.) mohri* n. sp.** (p. 84); *P. (P.) laie* (Barnard, 1970); *P. (P.) ornata* (Reid, 1951); *?P. (P.) saldanha* (Chilton, 1912); *P. (P.) schmidti* (Heller, 1866); *?P. (P.) thomsoni* (Hurley, 1957); *P. (P.) wolffi* (Reid, 1951); *P. (P.) darwini* (Barnard, 1979); *P. (P.) yaqui* (Barnard, 1979); *P. (P.) zuaque* (Barnard, 1979).
Macrodactyla subgroup: *P. (P.) chevreuxi* (K. H. Barnard, 1916); *P. (P.) honoluluensis* (Schellenberg, 1938); *P. (P.) macrodactyla* (Stebbing, 1899); *P. (P.) guasave* (Barnard, 1979).

Diagnosis: Small to medium hyalid species. Eyes round to subovate. Antenna 1, peduncular segment 2 reduced, little or not longer than segment 3.

Mandibular left lacinia 6-7 dentate; right lacinia bifid, may have accessory tooth. Maxilliped palp occasionally sexually dimorphic: unguis may be an elongate seta (male).

Coxae 1-3 with weak posterior marginal shelf, lacking cusps. Coxa 4, posterior margin smooth or with weak (vestigial?) cusp. Coxal gills sac-like.

Gnathopod 1, basal and ischial segments with well developed anterodistal (hydrodynamic) lobes in male, variously present (or lacking) in females; dactyl normal, not bifid or compound. Gnathopod 2 with large basal and ischial lobes (male), weak or lacking in females.

Peraeopods 3-7, segment 6, opposing margins spinose, with paired, often striated, distal clasping spines; dactyls simple, strong.

Epimeral plate 1 rounded behind. Pleopods well developed. Uropod 1, distolateral peduncular spine strong. Uropod 2, rami unequal. Uropod 3, peduncle with 2-5 posterodistal spines.

Telson lobes typically longer than wide, subtriangular, apically acute.

Female: Brood plate of gnathopod 2 broad, distally rounded or subacute, marginal hooked setae medium to long (> 1.2/ plate width). Preamplexing notch sharply incised, unguisial groove typically deep, broad, oblique.

Distribution: Cosmopolitan along tropical and warm-temperate marine shores, in algae at LW and shallow subtidal levels.

Remarks: The nominate subgenus *Protohyale* is distinguished mainly by the short peduncular segment 2 of antenna 1, the 6-7 dentate mandibular left lacinia, well developed hydrodynamic lobes of gnathopods 1 & 2 (males), and posteriorly rounded epimeral plate 1.

Protohyale (Protohyale) frequens (Stout)
(Fig. 37)

Allorchestes frequens Stout, 1913: 650
?Hyale frequens Shoemaker 1942: 16.
Hyale frequens (part) Barnard & Karaman 1991: 370.
Hyale nigra Barnard 1962:153. figs. 19, 20
Hyale rubra frequens Barnard 1969b: 139-141 (part?).
Protohyale frequens Bousfield 2001a: 104 (part).

Taxonomic clarifications: *P. (Protohyale) frequens* (Stout, 1913) is not conspecific with the following taxa:
1. Hyale rubra (Thomson) (Hurley and/or Barnard figs. of material from Australia, N. Zealand and S. America).
2. *Hyale frequens* Barnard 1952:23 (Central California); Barnard, 1954: 23 (Oregon). Both appear referable mainly to *P. (Boreohyale) lamberti* n. sp. (p. 62).
3. *Hyale rubra frequens* Barnard 1964:109, fig. 21A (Bahia de San Quintin, Baja California);—Barnard, 1969a: 212 (Bahia de Los Angeles, Baja California). The material was redescribed as *Hyale canalina* Barnard,1979, and treated here (p.84) as *P. (Protohyale) canalina* (Barnard, 1979).
4. *Hyale niger* (Haswell, 1879) (Australia).

Material Examined: CMN collections, including material on loan, contain no material of *P. frequens* (Stout, 1913) sens. str.

Diagnosis: Male (9.0 mm.): Anterior head margin oblique, nearly straight. Eyes medium, irregularly round Antenna 1, peduncular article 2 short, subequal to 3; segment 3 not exceeding distal end of peduncle 4 of antenna 2; flagellar segments each bearing 2 aesthetascs. Antenna 2 medium long, more than twice length of antenna 1; peduncular segments 4, 5 with posterodistal clusters of setae; flagellum 33-segmented, 2.3 times as long as peduncle.

Upper and lower lips regular. Mandible, left lacinia 6-dentate, with 3 accessory blades. Right mandible with 2 accessory blades. Maxilla 1, palp extending beyond base of apical spine teeth on outer plate. Maxilla 2, inner plate apically with inner marginal pectinate setae, proximal plumose seta elongate. Maxilliped, palp medium stout; dactyl not longer than segment 3, unguis short.

Coxae 1-3, posterior marginal shelf shallow but distinct, lower margins shallowly convex, not crenulated. Coxa 4, posteroproximal excavation lacking median cusp. Coxa 5 aequilobate. Coxal gills sac-like.

Gnathopod 1, h.-d. lobe of basis medium, rounded; lobe of ischium weakly developed; carpal lobe medium, lower margin bearing 6-8 comb setae; propod subrectangular, upper and lower margins slightly convex, but lacking stout anterodistal spine, palm shallowly oblique, slightly convex; posterodistal spines short, slightly separated, distal portion of posterior margin with single group of short setae; dactyl with minute posterior marginal setules, slightly overlapping palm. Gnathopod 2, basis and ischium with broadly rounded overlapping hydrodynamic lobes; merus acutely produced; carpal lobe lacking; propod deeply subovate, slightly narrowing distally, anterior margin proximally with two short spines, palm oblique, slightly convex, with weak hinge tooth, slightly shorter than posterior margin having two very short setal groups; dactyl stout, with slight posterior marginal bulge near hinge.

Peraeopods 3-4 ordinary; segment 5 short; segment 6, posterior margin with 6-7 short spines; dactyls slender, curved, slightly small than those of peraeopods 5-7. Peraeopods 5-7, hind margin of basis rounded, crenulate, rounded, with slight notch and surge seta; segment 4 of peraeopod 5 short, little longer than segment 5; in peraeopods 6 & 7, segment 5 is distinctly shorter and segment 4; segment 6 with 4-5 singly inserted or paired anterior marginal short spines and distally a pair of clasping (locking) spines,

Epimeral plates 2 and 3, hind corners weakly acuminate. Uropod 1, peduncle with 3-4 outer marginal spines, and prominent distolateral spine; outer ramus with 3 marginal spines. Uropod 2, outer ramus with 2-3 marginal spines. Uropod 3, peduncle stout, with 2 posterodistal spines; ramus slender, tapering, shorter than peduncle, apex with 2-3 short spines.

Telson lobes longer than wide, each tapering to acute apex, margins unarmed.

Female ov (7.0 mm): Gnathopod 1, hydrodynamic lobe prominent, rounded on basis, weakly developed on ischium; carpal lobe small, with few marginal comb setae; propod slender subrectangular, palm short, oblique, distal half of posterior margin with single group of short setae; dactyl slightly overlapping palm. Gnathopod 2 very similar to gnathopod 1. Brood plates and preamplexing notch originally undescribed, but probably similar to those of *P. (P.) mohri* (p. 81).

Distributional Ecology: Barnard (1969b) gives the range of *P. (P.) frequens* as Carmel to La Jolla and Laguna Beach, California, dominant among seaweed at the low water level. However, material listed from the central California region (north of Pt. Conception) and Oregon, not re-examined in this study, is probably synonymous with the superficially similar hyalid species *P. (Boreohyale) lamberti* n. sp. that occurs commonly in CMN collections from northern California to Southeastern Alaska (p. 62).

Remarks: *Protohyale frequens* (Stout) is the type species of the more advanced subgenus *Protohyale* that on the North American Pacific coast occurs mainly south of Pt. Conception, including Baja California and the Gulf of California. Species are characterized by

KEY TO NORTH PACIFIC SPECIES OF *PROTOHYALE (PROTOHYALE)*

(excluding *P. rubra* fide Barnard, and *Protohyale* sp. 2 Hirayama or *Protohyale*, spp. N. America)

1. Gnathopod 2 (♂), anterior margin of propod proximally with 1-4 short spines ..... 8.
   Gnathopod 2 (♂), anterior margin of propod lacking short spines ..... 2.

2. Gnathopod 2 (mature ♂), propodal palm elongate, very oblique; dactyl elongate, tip closing at level of merus; gnathopod 1 (♂), propod deep ..... 3.
   Gnathopod 2 (♂), propod palm short, regularly oblique, dactyl not elongate; gnathopod 1 (♂), propod regularly elongate, sub rectangular ..... 4.

3. Epimeral plates 2 and 3, hind corners acutely produced (Hawaii). ..... *P. (P.) honoluluensis* (Barnard)
   Epimeral corner 3 weakly acute (Central American mainland). ..... *P. (P.) guasave* (Barnard) (p. 86)

4. Antenna 2, flagellum short (<20 segments), proximal segments setose; uropod 1, outer ramus lacking marginal spines; telson lobes short, not longer than wide ..... *P. (P.) zuaque* (Barnard) (p. 86)
   Antenna 2, flagellum long (>25 segments), proximal segments smooth; uropod 1, outer ramus with 2 marginal spines; telson lobes longer than wide ..... *P. (P.) corallinacola* (Hirayama) (p. 86)

5. Antenna 2, flagellum short (<20 segments); gnathopod 2 (♂), propodal palmar tooth large, acute; gnathopod 1 (♂), propod as deep as long ..... *P. (P.) liae* (Barnard)
   Antenna 2, flagellum long (> 25 segments); gnathopod 2 (♂) propodal hinge tooth weak or lacking; gnathopod 1 (♂), propod regularly elongate subrectangular ..... 6.

6. Uropod 1, peduncular distolateral spine short (1/4 outer ramus); uropod 3, ramus long (> 2/3 peduncle) .... *P. (P.) frequens* (Stout) (p. 79)
   Combination not so; distolateral spine elongate (> 1.3 length of outer ramus). ..... 7.

7. Gnathopod 2 (♂), propod with 1 anterior marginal spines; palmar margin smooth; uropod 3, ramus short, length ~ 1/2 peduncle ..... *P. (P.) yaqui* (Barnard) (p. 85)
   Gnathopod 2 (♂), propod with 3 anterior marginal spines; propodal palm with weak rounded hinge tooth; uropod 3, ramus long (~2/3 peduncle) ..... *P. (P.) darwini* (Barnard)

8. Uropod 3, peduncle with 4-5 posterodistal spines; mandibular left lacinia 6-dentate; maxilliped, palp segment 4 (dactyl) lacking apical setae. ..... ***P. (P.) mohri*** n. sp. (p. 81)
   Uropod 3, pedun le with 2 posterodistal spines; mandibular left lacinia 51/2 dentate; maxilliped palp, dactyl with strong spical setae ..... *P. (P.) canalina* (Barnard) (p. 84)

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relatively short antennae and strongly developed hydrodynamic anterodistal lobes of the bases and ischium of the gnathopods of males and often on the bases of gnathopods of females. In these respects the species is markedly different from its northern counterpart *P. (B.) lamberti* (p. 63).

Some variation in gnathopods 1 & 2 in material from central California was noted and illustrated by Barnard (1962), reproduced here. As the illustrations are unaccompanied by other corresponding diagnostic character states, these variations are difficult to assign taxonomically. Thus, some appear similar to gnathopod character states of various species of subgenus *Boreohyale* (e.g., *P. (B.) jarrettae*, *P. (B.) seticornis*) that range southward from British Columbia into southern Oregon and northern California. Confirmation of their identification awaits reexamination of Barnard's original material and possibly other, yet unnamed Californian species of that subgenus.

Protohyale frequens is related also to *P. rubra* (Thomson, 1880) from Australia (see Barnard 1962, 1969b, 1979). However, North American material may be distinguished from species of the southern hemisphere by character states outlined and illustrated by Barnard (loc. cit.) and in the present keys (p. 82).

Protohyale (Protohyale) mohri n. sp.

(Fig. 38)

Protohyale lagunae (Stout, 1913) (erroneous attribute in Bousfield 2001a: 104)

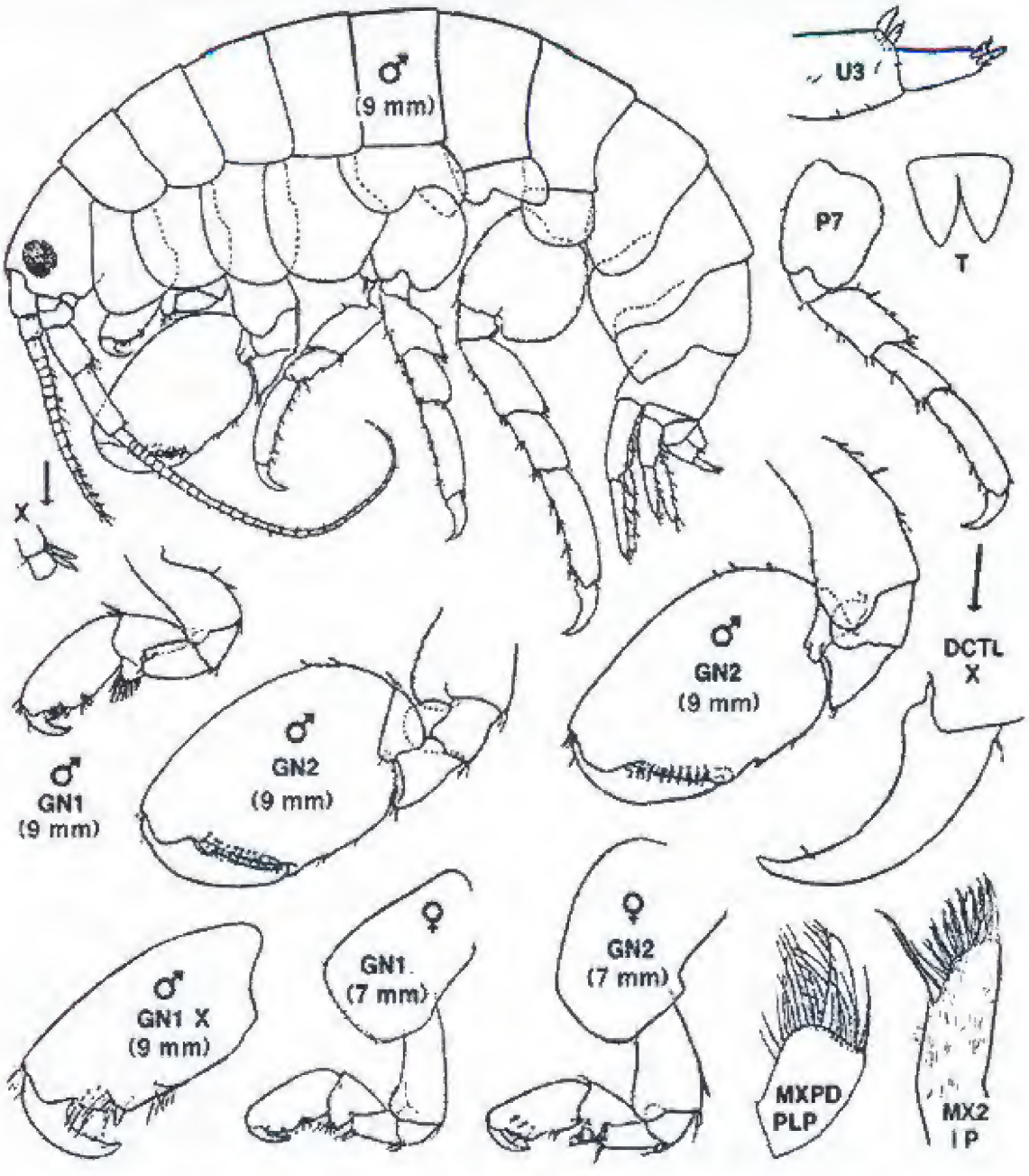

Fig. 37. *P. (Protohyale) frequens* (Stout, 1913). Male (9.0 mm); female ov (7.0 mm). Carmel to La Jolla, California (modified from Barnard 1962).

Material Examined:
CALIFORNIA.
Laguna Beach, North Reef, in slender eel grass (*Phyllospadix*), J. L. Mohr coll., Jan. 24, 1948. ♂ (5.5 mm) **Holotype** (slide mount); ♀ ov (4.5 mm) (**Allotype**) (slide mount), 5 ♂♂, 9 ♀♀, 6 im. (**Paratypes**), USNM loan No. 180284.

Diagnosis: Male (5.5 mm.) Body small to medium. Eyes small, subcircular. Antenna 1, peduncular segment 2 short, little longer than 3; segment 3 not exceeding distal end of peduncle 4 of antenna 2; flagellum 12-13 segmented, each bearing 2 aesthetascs. Antenna 2 relatively about twice length of antenna 1; peduncular segments 4 & 5 bare; flagellum of 25-27 smooth segments.

Upper and lower lips sparsely pilose distally. Mandible, left lacinia 6-dentate, spine row with 3 accessory blades; right mandible with 2 accessory blades. Maxilla 1, palp slender, tip extending beyond base of apical spine teeth of outer plate. Maxilla 2 regular; inner plate with inner apical row of pectinate setae. Maxilliped, outer plate short, rounded distally; palp stout; dactyl

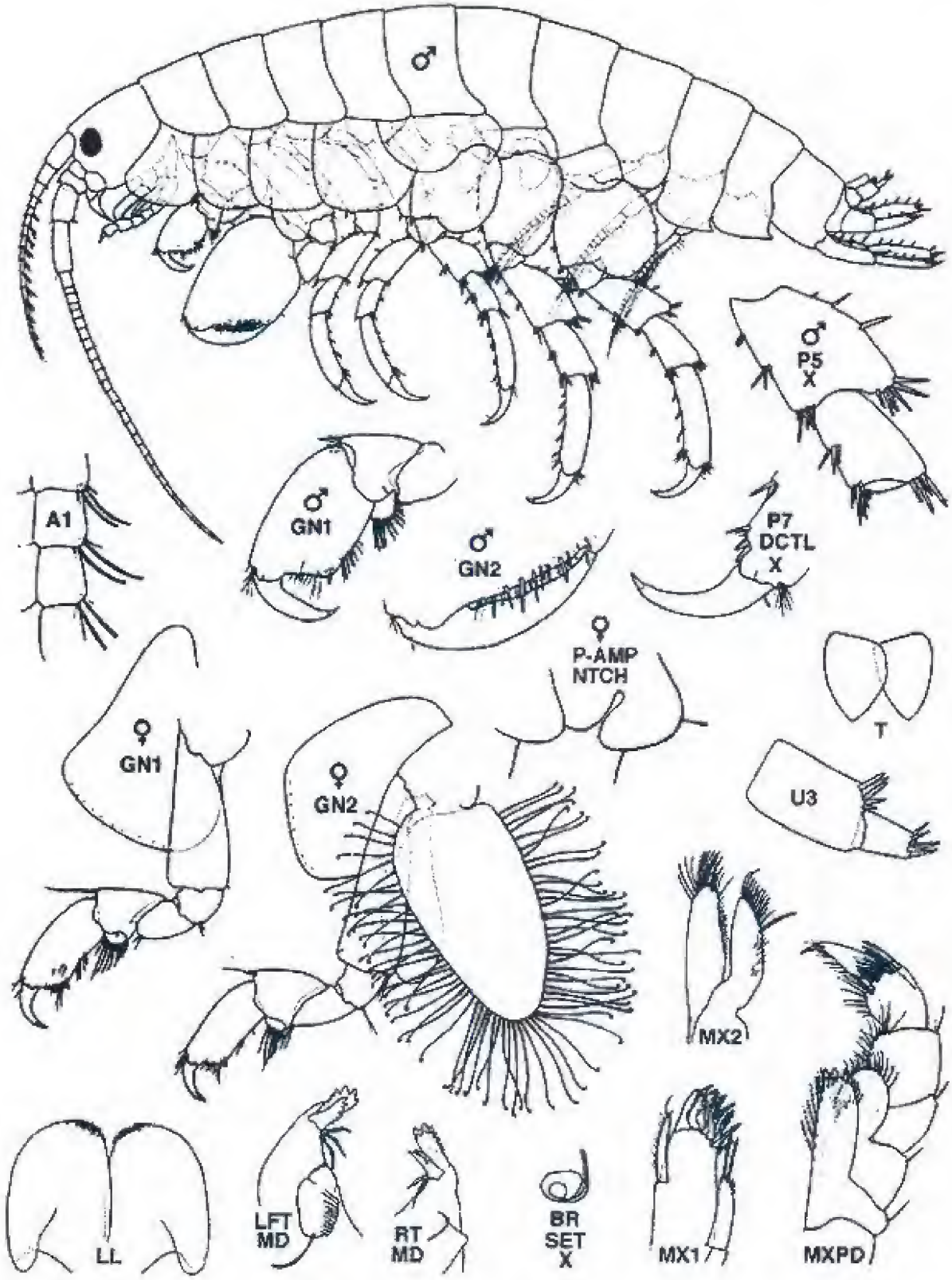

Fig. 38. ***P. (Protohyale) mohri*** **n. sp.** Male (5.5 mm); female ov (4.5 mm). North Reef, Laguna Beach, California.

slightly longer than segment 3, inner margin setose, unguis not elongate.

Coxae 1-3, posterior marginal shelf very weak or lacking, lower margins slightly convex, not crenulated. Coxa 4 with simple posteroproximal excavation, lacking median cusp. Coxal gills relatively small, sac-like, coxa 6 smallest.

Gnathopod 1, hydrodynamic lobe of basis distinct; weakly developed on ischium; merus rounded posterodistally; carpal lobe broad, shallow, bearing10-12 comb setae; propod subrectangular, lacking strong anterodistal spine, palm oblique, straight,posterodistal spines short, close set, distal portion of posterior margin with continuous row of ~8 short setae; dactyl simple, stout, with 6 minute posterior marginal setules. Gnathopod 2, hydrodynamic lobe of basis large, rounded; virtually lacking on ischium; merus normally extended; carpal lobe lacking; propod deeply subovate, narrowing slightly distally, anterior margin with 2 spines, palm oblique, shorter than posterior margin,nearly straight, with weak hinge tooth; dactyl with slight inner marginal bulge near hinge.

Peraeopods 3-4 slender, segment 5 short; segment 6, posterior marginal spines increasing distally to paired weakly striated locking spines. Peraeopods 5-7, hind margin of basis rounded, crenulate,each with notch and surge seta; segment 5 shorter than 4, little broadened distally; segment 6 with 4-6 medium strong single or doubly inserted anterior marginal spines; dactyls strong.

Epimeral plates 2 & 3, hind corners acuminate. Pleopods regular, natatory. Uropod 1, peduncle with (3-4) outer marginal spines; distolateral spine one-third length of outer ramus having 3 marginal spines. Uropod 2, outer ramus with 2 marginal spines. Uropod 3, peduncle stout, with 5-6 posterodistal spines; ramus short, apex blunt, with 6 spines.

Telson, lobes slightly longer than broad, margins smooth.

Female ov (4.5 mm.): Gnathopod 1, basis with small hydrodynamic lobe; carpal lobe shallow, broad, with ~8 long comb setae; propod slender, subrectangular, slightly curved; palm short, oblique, distal half of posterior margin with 2 small groups of short setae; dactyl slightly overlapping palmar spines. Gnathopod 2 very similar to gnathopod 1, except carpal lobe smaller, with fewer comb setae.

Brood plate of gnathopod 2 short, subovate, broadly rounded apically, margins with ~70 long hooked setae. Pre-amplexing notch of peraeon segment 2 strongly incised; unguisial groove broad, straight, oblique; posterodistal lobe shallow, sharply rounded anteriorly.

Etymology. The species is named in honour of Dr. John L. Mohr, University of Southern California,and Allan Hancock Foundation, collector of the type material.

Distributional Ecology: Known only from the North reef at Laguna Beach, southern California; in slender eel grass at LW level.

Remarks: The type lot contains an original identification label of C. R. Shoemaker as "*Hyale frequens*", that contributed in part to the erroneous authorship attribute of Bousfield (2001a) as *Protohyale lagunae* (Stout, 1913). The species is clearly a member of the advanced subgenus *Protohyale* that occur mainly south of Pt. Conception along the coasts of Baja California, and in the Gulf of California. In *P. (P.) frequens*, hydrodynamic lobes of the ischium of gnathopods 1 and 2 of the female are not developed.

Protohyale (Protohyale) canalina (Barnard)
(Fig. 39)

Hyale canalina J. L. Barnard, 1979: 102, fig. 56 (part)
Hyale rubra rubra Barnard 1969b: 138.
Protohyale canalina Bousfield 2001a: 104.

Diagnosis: Male (6.3 mm). Eyes medium. Antenna 1, peduncle 2 short, flagellum medium, 14-15 segmented, with 1-2 aesthetascs per segment. Antenna 2, peduncle and flagellum nearly bare, flagellum 28-segmented.

Mandibular left lacinia not described; right lacinia evenly bifid, with accessory side tooth; spine row with 3 blades. Maxilliped palp slender, inner lobe narrow, setose distally; dactyl slender, elongate, unguis short, with tuft of long apical setae.

Coxal plates 1-3 lacking posterior marginal cusps. Coxa 4, posterior excavation with weak marginal cusp. Coxal gills not described.

Gnathopod 1, basis with strong anterodistal hydrodynamic lobe, weakly developed on ischium; carpal lobe sharply rounded, margin with 10-12 comb setae; propod narrowing distally, posterior margin with proximal row of 4 short setae and distally uneven row of five longer setae; palm short, convex, overhung by strongly curved minutely ridged dactyl. Gnathopod 2, basis

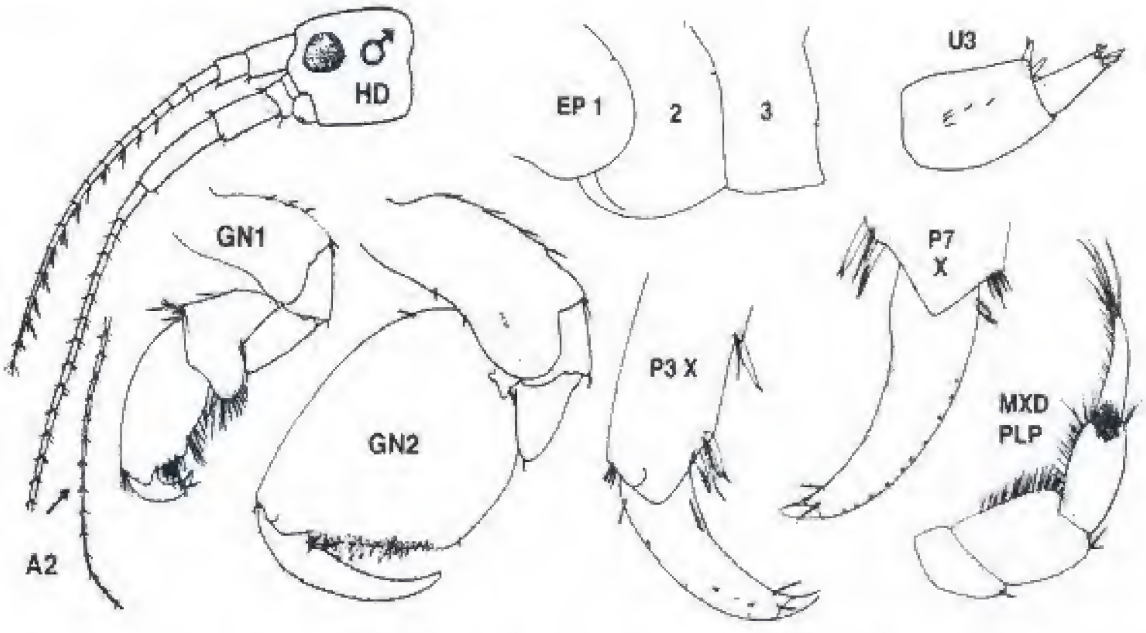

Fig. 39. *P. (Protohyale) canalina* (J. L. Barnard, 1979). Male (6.3 mm). Santa Catalina I. to Isla Cedros, Baja California. (modified from Barnard 1964, 1969b, 1979).

with 4 posterior marginal stiff setae,and very large and broadly rounded anterodistal lobe; ischial lobe strong, sharply rounded; propod large, relatively short and deep, with 1-2 spines proximally on anterior margin, posterior margin gently convex, palm oblique, straight, with low hinge tooth, lined with with stiff setae; dactyl slender, with weak proximal inner marginal hump.

Peraeopods medium strong, regular, segment 6 with paired short straight striated locking spines distally near base of dactyl; dactyl medium large, inner margin castellate proximally and with small seta distally.

Epimeron 1 rounded behind, 2 & 3 with weakly acuminate hind corners. Uropod 1 with strong distolateral peduncular spine; rami of uropods 1 & 2 regularly marginally spinose. Uropod 3, peduncle with 2 posterodistal spines; ramus short, with 5 apical spines.

Telson lobes ordinary (presumably apically acute, length and width subequal).

Female: gnathopods, broods plates, and pre-amplexing lobe undescribed but presumably similar to *P. yaqui* (see below).

Distributional Ecology: Santa Catalina I. and offshore Californian archipelago, to Isla Cedros, Baja California, Mexico, in *Phyllospadix* mats, lower intertidal.

Remarks: In addition to its overall similarity to *P. (P.) frequens* and *P. (P.) mohri* from the open coast of southern California, *P. (P.) canalina* is closely related to two other species from Baja California and the Gulf of California. All have well developed hydrodynamic lobes on basis and ischium of gnathopods 1 and 2 especially in the ♂ (see Barnard (1979) and key, p. 81): (1) *P. (P.) yaqui* Barnard, 1979, has been recorded from Bahia San Quintin (open coast below the southern California border), and widely in the Gulf of California at Estero dePunta Banda, Bahia de Los Angeles, and Puerto Penasco (type locality). The species name was required to accommodate "*Hyale nigra*" (bay form) of Barnard (1964), and "*Hyale rubra frequens*" of Barnard (1967). Some aspects of the female of *P. (P.) yaqui* had not been illustrated and described by Barnard (1979); a female specimen (6.0 mm) from Bahia San Quintin (CNM collections) was examined and some additional features included in a reorganized plate of the original excellent outlines of Barnard (1979) (fig. 41). The examination confirmed well developed hydrodynamic lobes of the basis and ischium of gnathopod 1 and basis of gnathopod 2 in both males and females, the slight posterior marginal cusp of coxa 4, and the strongly developed distolateral peduncular spine of uropod 1. The inner plate of maxilla 2 was armed distally with 9 pectinate setae and ~12 simple setae, in addition to the large stout proximal marginal plumose seta. Also present were large subovate brood plates with elongate marginal hook-tipped setae. The preamplexing notch of peraeon segment 2 of the female of *P. (P.) yaqui* was marked by a deep oblique unguisial groove, and a posterior lobe with sharply rounded anterodistal margin, similar to that in *P. (P.) mohri* (fig. 38), and other species within the subgenus *Protohyale*.

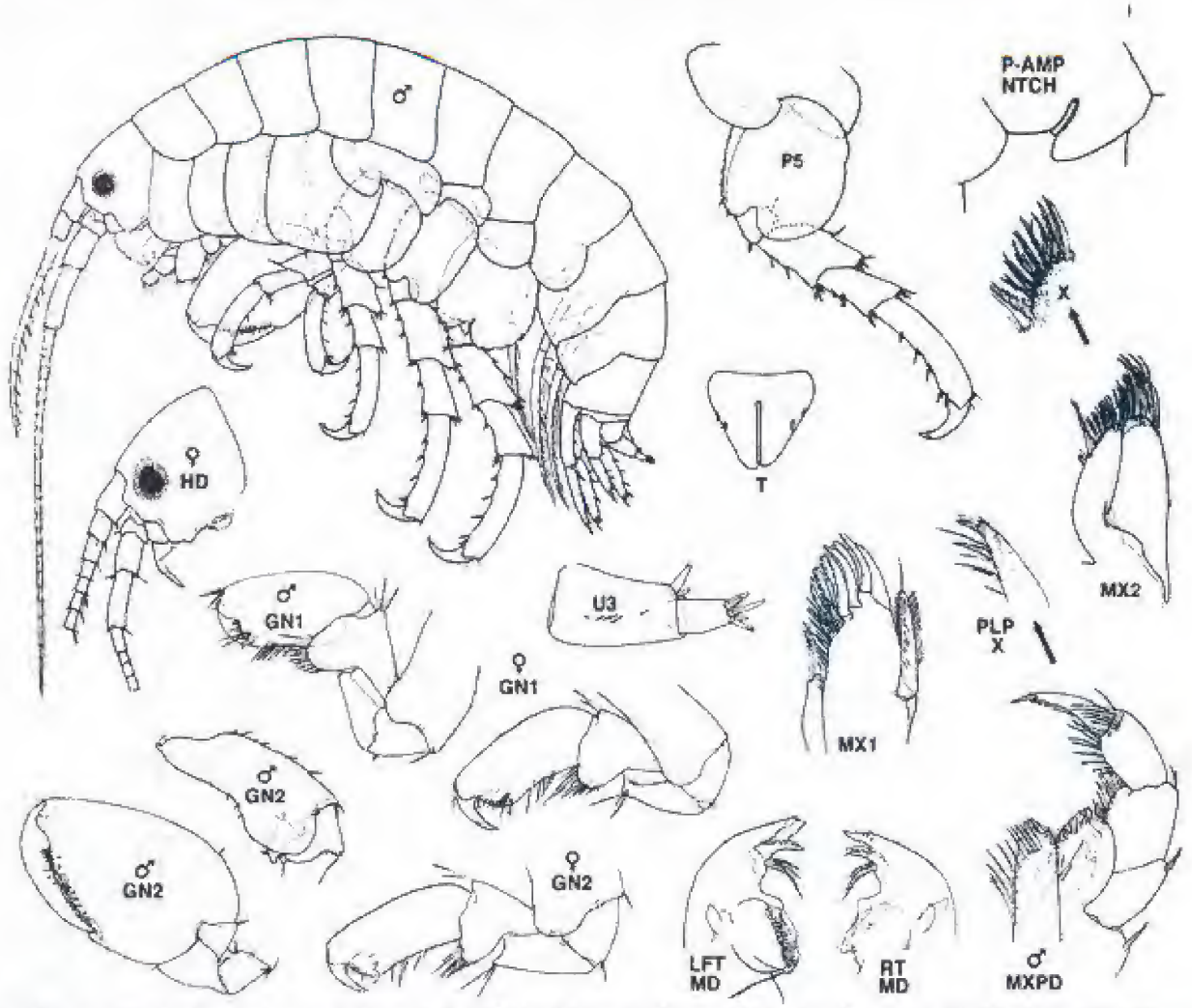

Fig. 40. *P. (Protohyale) yaqui* Barnard, 1979. Male (6.2 mm) Puerto Penasco,Gulf of California. Female ov (4.2 mm), Puerto Penasco, and Bahia (modified from Barnard 1979); female ov. (6.0 mm) Bahia de San Quintin, B. C. (maxilla 2 enlargement, and pre-amplexing notch from CMN collections).

(2) *P. (P.) zuaque* Barnard, 1979, has been recorded intertidally from near Cabo San Lucas, Baja California. The species differs from *P.yaqui* and *P.canalini* in its shorter, lightly setose antenna 2, stronger inner marginal shelf on maxilliped palp segment 3, and more elongate distolateral peduncular spine of uropod 1.

Also recorded from the Cabo San Lucas region is *P. (P.) guasave* (Barnard, 1979) (Fig. 40). However, in the elongate distally narrowing setose form of the male gnathopod, and the relatively large deep propod of gnathopod 1, this species more closely ressembles the Hawaian *P. (P.) honoluluensis* Schellenberg, 1938, *P. (P.) inermis* (Ledoyer, 1979a) and other species of the "*macrodactyla*" subgroup of Stebbing (1899). Other Hawaiian species more typical of the *P. (P.) frequens* group include *P. (P.) ayeli* (Barnard, 1955), and possibly *P. (P.) affinis* (Chevreux, 1908), partly illustrated by Barnard (1955), and *P. (P). laie* (Barnard, 1970). *P. (P.) darwini* (Barnard, 1979), from the Galapagos Ids., also appears to be a member of the *frequens* subgroup within subgenus *Protohyale*.

In the western Pacific region only one named species of subgenus *Protohyale* has yet been fully described. Several new forms are currently in preparation (Hiwatari, pers. comm.). Most clearly referable to the subgenus is *P. (Protohyale) corallinacola* (Hirayama, 1980) from Ishigaki I. in the East China Sea (Fig. 42). Samples of males of this small species are present in CMN collections, all having well developed hydrodynamic lobes , especially on the basis of gnathopods 1 and 2, but females are lacking. Consequently the form of the female gnathopods, brood plates, and preamplexing notch of peraeon segment 2 are yet unknown. These character states are also unknown for two unnamed species of subgenus *Protohyale*, described from the same region by Dr. Hirayama (1980).

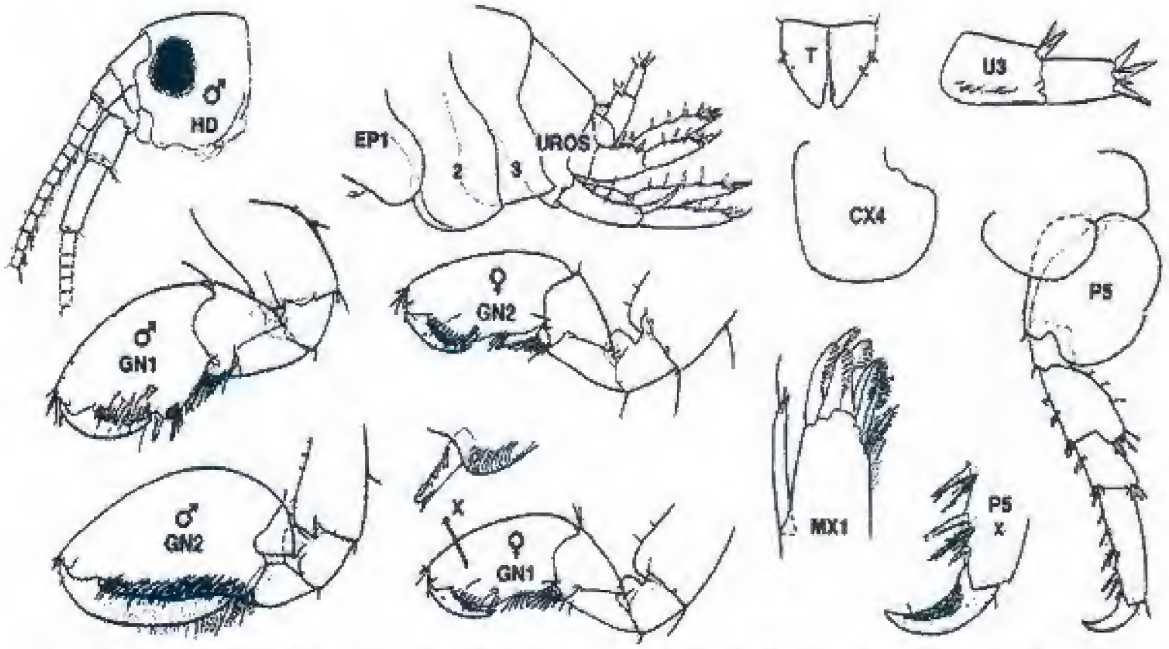

Fig. 41. *P. (Protohyale) guasave* (Barnard, 1979) Male (4.8 mm); female ov (4.0 mm). East of Cabo San Lucas, Baja California. in intertidal algae.

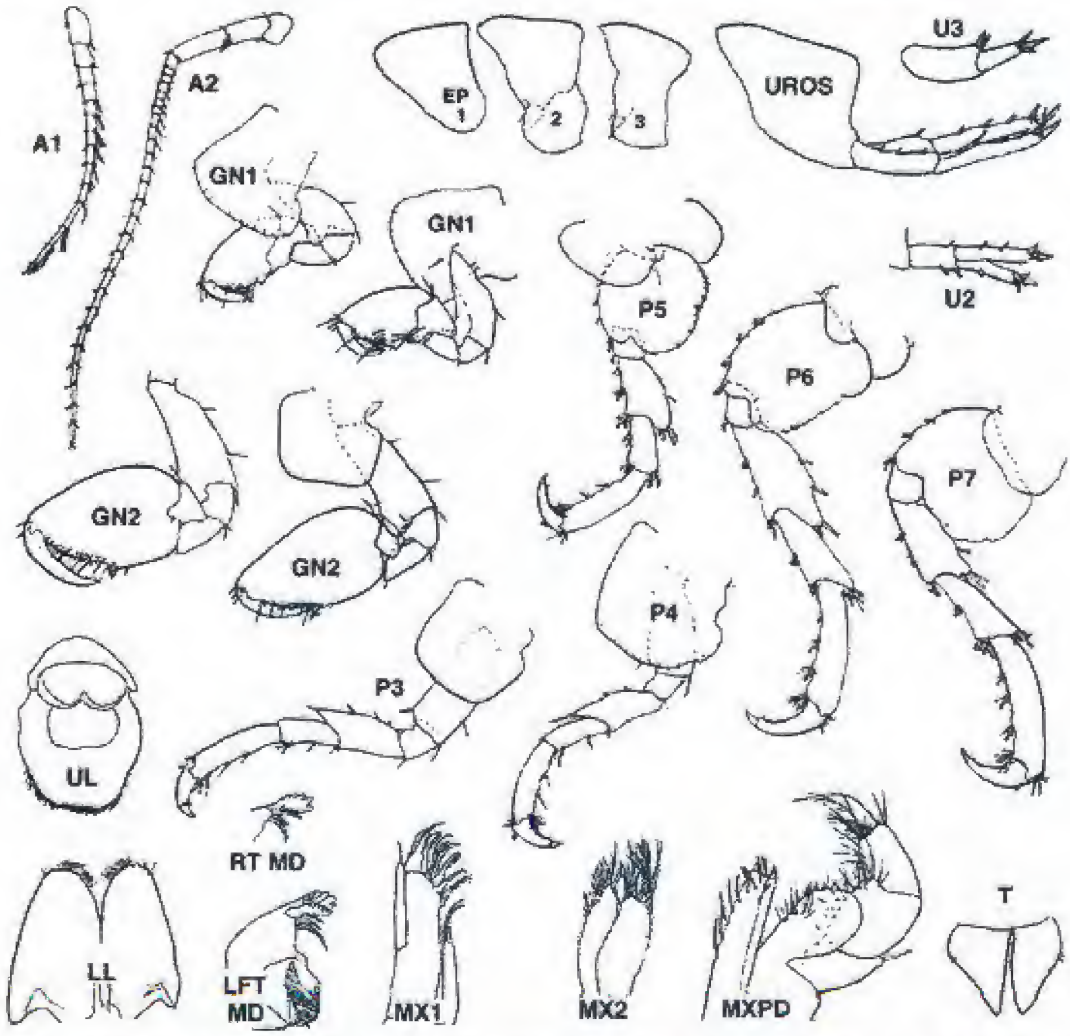

Fig. 42. *P. (Protohyale) corallinacola* (Hirayama, 1980). Male (4.2 mm). Ishigaki I., Ryukuku Ids., Japan.

Protohyale (Leptohyale) n. subg.

Type species: ***Protohyale (Leptohyale) longipalpa,*** n. sp. (monotypy).

Diagnosis: Small to medium protohyalids with moderate development of hydrodynamic lobes, specialized elongate maxilliped palp in male, and unequal dactyls of peraeopods 3-4 and 5-7.

Body smooth, small to medium in size. Eyes small, round, lateral. Antenna 1 short, peduncular segments short, flagellum short. Antenna 2, peduncular segment 4 distinctly shorter than 5; flagellum elongate, 25+ segmented, unarmed.

Upper and lower lips regular. Mandible: left lacinia 7-8 dentate, incisor 8-dentate, spine row with 2-3 slender blades. Maxilla 1, inner plate short, with single apical plumose seta; palp relatively short, 1-segmented, reaching base of apical spines of outer plate. Maxilla 2, inner plate with apical pectinate setae. Maxilliped strongly sexually dimorphic, palp (male), segment 2 longer than broad; dactyl elongate.

Coxae 1-4, lower margins rounded, posterior marginal shelf shallow. Coxa 4 broad, deep, rounded below, posterior excavation lacking median cusp. Coxa 5 weakly anterolobate. Coxae 6 shallowly posterolobate. Coxal gills relatively small, mostly saclike.

Gnathopods 1 & 2 sexually dimorphic. Gnathopod 1 (male) dissimilar in size and form to female; basis with medium hydrodynamic lobe; carpal lobe strong; propod subovate (subrectangular in female), lacking anterodistal spine(s), palm short; dactyl regular. Gnathopod 2 (male) large, powerfully subchelate; basis and ischium with large rounded overlapping hydrodynamic lobes; carpal lobe minute; propod, palm and dactyl each with low hinge tooth. Gnathopod 2 (female) similar in size and form to gnathopod 1, basis with hydrodynamic lobe.

Peraeopods 3-4 slender; segment 5 not shortened; dactyls relatively small. Peraeopods 5-7 slender ,bases unequally broadened, rounded hind margin weakly crenulated, with small notch and surge seta; segments 4 & 5 regular; segment 6, clasping spines paired but not enlarged; dactyls medium, distinctly larger than those of peraeopods 3 & 4, inner marginal seta weak or lacking.

Epimeral plates 1-3, hind corners weakly acuminate, lower margins unarmed. Pleopods regular. Uropod 1, peduncle and rami slender, subequal in length; peduncle with distolateral spine; rami with marginal spines. Uropod 2, rami unequal, with marginal spines. Uropod peduncle with 2 posterodistal spines; ramus slender, with apical spines only.

Telson lobes little longer than wide, margins smooth.

Female: Gnathopods 1 and 2, basis with hydrodynamoic lobe. Brood lamellae broadly subovate, apically rounded; marginal setae medium, hook-tipped. Pre-amplexing lobe with distinct unguisial groove.

Etymology: From the Greek *leptos* (thin) + *hyale*, alluding to the slender elongate distal segments of the maxilliped palp in the male.

Distributional Ecology: Known only from localities on the outer coast of southeastern Alaska and British Columbia, sparingly south to Oregon.

Remarks: The subgenus appears closest to *P. (Protohyale)* but shows a number of apomorphic characters states including the 8-dentate mandibular left lacinia, strongly sexually dimorphic gnathopods and maxilliped palp, and short broad telson lobes.

Protohyale (Leptohyale) longipalpa, n. sp.
(Fig. 43)

Leptohyale longipalpa Bousfield, 1981 (unpubl. MS); —Bousfield 2001a: 104 (nomen nudum)

Material examined:

ALASKA

ELB Stns, 1961: A175, west of Pt. Eugenia, San Juan Batista I., Alexander Archipelago, July 26 - ♂ (8.0 mm) **Holotype** (slide mount), CMNC 1983-1528.

ELB Stns, 1980: S11B1 (6♂♂, 20♀♀, 3 im); S20B2 (6 ♂♂, 5 ♀♀); S20B5 (1 ♂, 7 ♀♀, 1 imm).

BRITISH COLUMBIA

North Central Coast: ELB Stns 1964. H53, St. John Harbour, Athlone I. - 1 im.

Southern Vancouver I.: ELB Stn ,1970: P718, Becher Bay, 4 ♂♂, 4 ♀♀.

ELB Stn, 1976: B7 (1 ♂)

ELB Stn, 1977: B6a, Trial I., Victoria 1 ♂, 6 ♀♀.

Other B. C. material: H. Aston. Stn 612-10-1, Hecate Strait, 1992 - 1 ♀ ov (6.0 mm),(slide mount), NMCC Acc. A1991.0023. E. Black Stn, 1980: Deer Island, kelp bed, Aug. 20 - 1 ♀ ov (6.0 mm) **Allotype** (slide mount), CMNC 1983-1529; Ibid., Apr. 2, 1980 - ♂ (8.5 mm); Bear Cove, Sept. 25 - ♀ ov (4.0 mm), 1 im; North of Nanaimo, A. Schueler coll., summer, 1977 - 1 ♀ ov, NMCC Acc. No. 1978-144.

WASH-OREGON

ELB Stns, 1966: W60, Otter Rock, at Marine Gardens, ORE, 1 ♂, 13 ♀♀, 18 im.

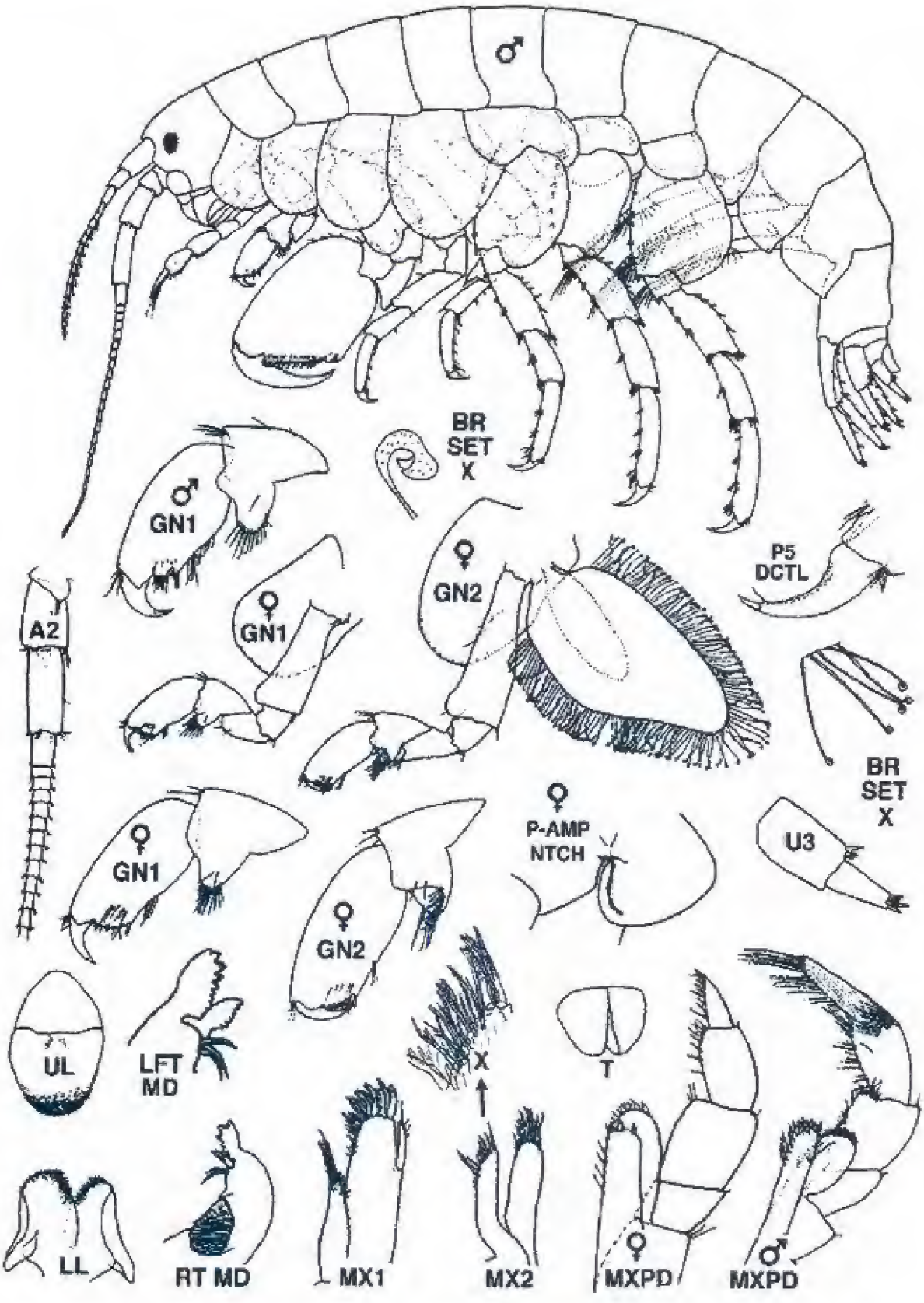

Fig. 43. *Protohyale (Leptohyale) longipalpa* **n. subg., n. sp.** Male (8.5 mm). San Juan Batista I., Southeastern Alaska. Female ov (6.0 mm). Deer I., B. C.

Diagnosis: Male (8.5 mm). Antenna 1, flagellum ~15-segmented; peduncle short, not extending past peduncle 4 of antenna 2; flagellar segments with posterior mariginal aesthetascs. Antenna 2, peduncular segments 4 and 5 stout; flagellum ~25-segmented, margins nearly bare.

Upper and lower lips with dense distal fine pilosity. Mandibles relatively small slender. Maxilla 1, outer plate, apical spine teeth slender. Maxilliped palp, facial surfaces of dactyl finely pectinate, with strong medial and apical setae.

Coxae 1-4 deeper than wide, lower margins strongly rounded. Coxal gills largest on peraeopod 6.

Gnathopod 1 relatively small; carpus, dorsal margin shorter than propod, armed with 1-2 stiff setae, posterior lobe rounded below, margin armed with 8-10 strong comb setae; propod subovate, narrowing distally, palm very short, oblique; dactyl short, tip simple, closing beyond stout posterodistal spines of propod; dactyl with distinct posterior marginal rounded tooth or swelling near hinge . Gnathopod 2, propod very large deeply subquadrate, anterior margin proximally with 4 short spines, lower margin with 1-2 short setae.

Peraeopods 3 & 4 slender, segment 5 slightly shorter than 6. Peraeopods 5-7, bases unequally broadened (6 narrowest); segment 5 slightly shorter than segments 4 & 6.

Uropod 1, peduncle with 2-3 outer marginal spines and short distal spine; rami each with 3 short marginal spines. Uropod 2, rami longer than peduncle each with 2-3 marginal short spines. Uropod 3, peduncle with 2-3 posterodistal spines; ramus tapering, about equal in length to peduncle, with 4-5 apical spines.

Telson lobes slightly narrowing to smooth, broadly rounded apices.

Female ov (6.0 mm): Maxilliped palp, dactyl regular, not elongate. Gnathopods 1 & 2 subsimilar; hydrodynamic lobe medium on basis, lacking on ischium; carpal lobe shallow; propod slender, subrectangular, palm short, oblique, hind margin with single distal row of 3-4 close-set setae; dactyl not overlapping palm. Brood plate (peraeopod 2) longer than basis, margin lined with ~150 relatively short hook-tipped setae (~one-third plate width). Preamplexing notch large, squared; unguisial groove short, wide, slightly arched; posterodistal peraeonal lobe shallow, anterior margin evenly rounded. Peraeopods 3-7 are relatively short, with more broadly expanded segments 4 & 5 of peraeopods 5-7. Some morphological variation was noted but is not considered of species significance.

Etymology: The species name alludes to the elongated palp of the maxilliped of the male.

Distributional Ecology: From southeastern Alaska sparsely through British Columbia to Washington and Oregon; among algae, LW to immediately subtidal.

***Protohyale (Diplohyale)* n. subg.**

Hyale complex Barnard & Karaman 1991(part): 367.

Type species: *Hyale diplodactyla* Stebbing,1899 (present designation).

Species: *Diplohyale bidentata* (Ledoyer, 1984; 97, fig. 47); *D. dentifera* (Chevreux, 1907, 1908) (J. L. Barnard, 1965); *D. didendactyla* (Hirayama, 1980: 131, figs. 1-3); *D. diplodactyla* (Stebbing,1899: 403, t. 31C), (Stebbing 1906: 562, fig. 95), (Sivaprakasam 1969) (Ledoyer 1979b).

Diagnosis: Like *P. (Protohyale)* except dactyl of gnathopod 1 (mature male) with a strong tooth on the posterodistal margin (bidentate) (fig. 44).

Body small (3-5 mm), smooth. Eyes medium, broad, ovate, lateral. Antenna 1 short, peduncular segments 2 and 3 short; flagellum short (<10 segments). Antenna 2, peduncle 4 short; flagellum variable in length, proximal segments may have very short posterior marginal setae.

Mandible, left lacinia 6-dentate, spine row with 3 blades. Maxilla 1, palp relatively long, 1-segmented, extending beyond base of outer plate apical spines. Maxilla 2, inner plate with single short inner marginal plumose setae. Maxilliped, inner plate subrectangular; outer plate distally rounded; palp stout, segments 2 and 3 broad; dactyl regular, unguis short.

Coxae 1-3 lacking posterior marginal cusps. Coxa 4, margin of posterior excavation with weak medial cusp. Coxa 5 anterolobate. Coxae 6 and 7 posterolobate. Coxal gills subovate, largest posteriorly.

Gnathopod 1 (male) larger than, and dissimilar in form to female; hydrodynamic lobe of basis small or lacking; carpal lobe distinct; propod broadening distally; palm distinct, oblique; dactyl strongly bidentate, distal tooth closing between anterodistal palmar spines. Gnathopod 2 (male) powerfully subchelate, regular; basis and ischium with regular hydrodynamic lobes; carpal lobe lacking; propod subovate, palm various, oblique, with weak hinge tooth; dactyl regular.

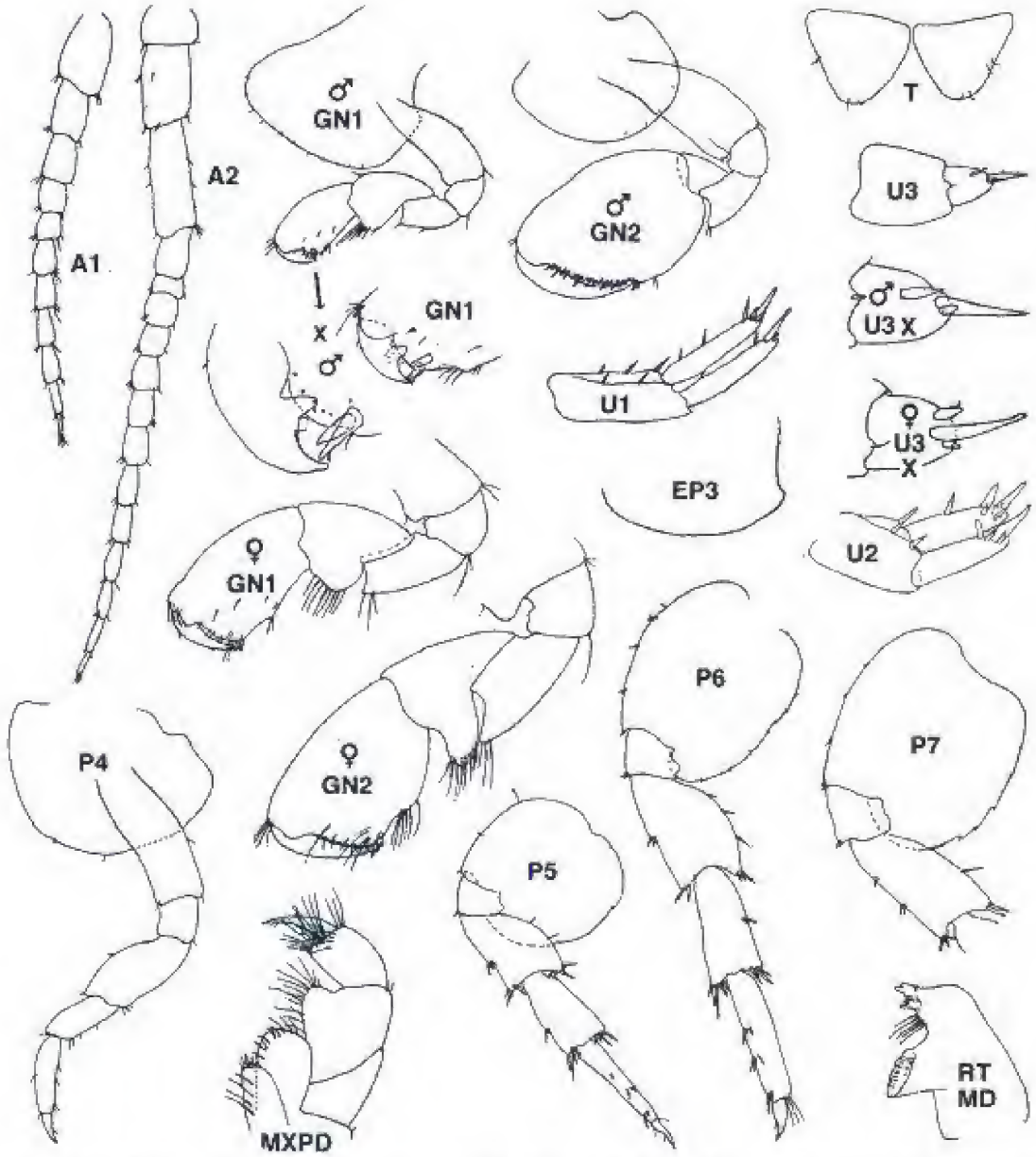

Fig. 44. *Protohyale (Diplohyale) bidentata* (Ledoyer, 1984), Male (3.0 mm); female (3.0 mm). New Caledonia (after Ledoyer 1984).

Peraeopods 3-7, various but not stout; bases medium broad, rounded hind margin slightly crenulated, notch and surge seta weak; segment 4 of peraeopod 5 slightly broadened; segment 6, clasping spine distinct but not enlarged or striated; dactyls medium, inner marginal seta very weak or lacking.

Epimeral plates smooth below, hind corners acuminate to slightly produced; plate 2 deepest. Pleopods well developed, rami normal. Uropod 1, peduncle shorter than rami, with strong distolateral spine; rami, marginal spines few or lacking, apical spines strong. Uropod 2, outer ramus shorter, marginal spines few. Uropod 3 uniramous (inner ramus a trace fused to peduncle); ramus usually shorter than peduncle, with strong apical spines.

Telson lobes triangular, usually longer than wide, apical margins smooth.

Female: Gnathopod 2 somewhat dissimilar in size and form to gnathopod 1. Brood lamellae and pre-amplexing notch not described.

Etymology: From the Greek *diploos* - twofold + *hyale*, alluding to the touble-toothed form of the dactyl of gnathopod 1 (male).

Distributional ecology: Mainly at LW and subtidal levels of surf coasts of the Caribbean, western Pacific (Japan), and Indo-Pacific (New Caledonia to Moluccas).

P. (Diplohyale) bidentata (Ledoyer)
(Fig. 44)

Hyale bidentata Ledoyer, 1984: 97, fig. 47; Barnard & Karaman 1991: 369.

This small species shows a number of character states that link the genus *Protohyale* to other hyalid genera. Thus, a weak posterior marginal cusp is present on coxa 4 (as in *Parhyale*), segment 4 of peraeopods 5-7 is somewhat broadened (as in *Lelehua*), and in uropod 3, the remnant of an inner ramus is fused to the peduncle (as in *Parhyale* and *Ptilohyale).*

Unfortunately, little can be deduced from published species accounts concerning the form of the coxal gills and brood plates. Nothing is known of the form of the preamplexing notch. Paratype material of Hirayama and Hiwatari in CMN collections contains only males.

Lelehua J. L.Barnard

Hyale (Lelehua) J. L. Barnard, 1970: 264.
Lelehua Barnard 1974: 58;—Barnard & Karaman 1991: 370.

Type species: *Lelehua waimea* Barnard, 1970, original designation.

Species: *Lelehua ishigakiensis* Hirayama, 1980: 179, figs 7-9; *L. kandari* Barnard, 1974: 55, figs. 36, 37; *L. malevua* Myers, 1985; *L. inermis* Ledoyer, 1978: 317, fig.43.

Diagnosis: Body small (3-5 mm), smooth. Eyes rounded, lateral, medium. Antenna 1 short, peduncular segments 2 & 3 short, flagellum short (<10 segments). Antenna 2, peduncle short; flagellum medium short (<20 segments), smooth.

Mandible, left lacinia 5-dentate, spine row with 2-3 blades. Maxilla 1 palp 1-segmented, long, extending beyond base of outer plate apical spines. Maxilla 2, inner plate with single inner marginal plumose seta. Maxilliped, outer plate distally subacute; palp, segment 2 longer than broad; dactyl usually sexually dimorphic (unguis (♂)elongate, forming a "whip seta").

Coxae 1-3, posterior marginal cusps lacking. Coxa 4, posterior excavation lacking distinct cusp. Coxa 5 aequilobate. Coxae 6 & 7 posterolobate. Coxal gills not described.

Gnathopod 1 (♂) larger and slightly different in form to female; carpal lobe distinct, relatively broad, shallow; propod slightly broadening distally (more elongate in female),apparently lacking median facial guiding spine; palm short but distinct, oblique; dactyl simple (or unguis slightly bifid). Gnathopod 2 (♂) powerfully subchelate, often with hinge tooth; basis with medium hydrodynamic lobe; carpal lobe lacking; propod subrectangular to broadly subovate, palm strongly oblique, variously incised medially; dactyl stout,with inner marginal swelling or low tooth.

Peraeopods 3-7 usually stout; bases medium broad, rounded hind margin weakly crenulated, with notch and surge seta ; segment 4 broadly expanded, wider than long; segment 5 short to medium; clasping spine (segment 6) distinct but not enlarged; dactyl medium large, inner marginal seta small.

Epimeral plates smooth below, hind corner weakly acuminate; plate 2 deepest. Pleopods well developed, rami normal. Uropod 1, peduncle shorter than rami, with strong distolateral spine, marginal spines of outer ramus few or lacking, apical spines strong. Uropod 2 rami unequal, marginal and apical spines few but relatively strong. Uropod 3 short, uniramous; ramus shorter than peduncle, with apical spines only.

Telson lobes triangular, medium to long, apical margins smooth.

Female : Gnathopod 2 regular, similar to but larger than gnathopod 1. Brood lamellae and preamplexing notch not described.

Distributional Ecology: Warm-temperate and tropical waters of the western North Pacific to Japan & the IndoPacific region; mainly along exposed coastlines, from LW level to depths of 30 m, on *Poccilopora* sp., (Barnard 1970).

Remarks: The original generic distinction was based on the sexually dimorphic palp of the maxilliped which Barnard (1970, p. 268) correctly predicted might be found in other species of *Hyale* (sens. lat). Four additional species are recognized here, all described subsequent to Dr. Barnard's original diagnosis of the type species (1970). *L. ishigakiensis* Hirayama (Fig. 45) is strikingly similar to *L. waimea* of the Hawaiian Island archipelago, with which it is considered a counterpart species (Table IV).

The genus *Lelehua* also shows some character state similarities with *Micropythia* and *Hyale* sens. str., including the oval eye, short antennae, markedly broadened segment 4 of peraeopods 5-7, and subtidal habitat. However, *Lelehua* differs in its strongly sexually dimorphic maxilliped; strongly excavate palm of gnatho-

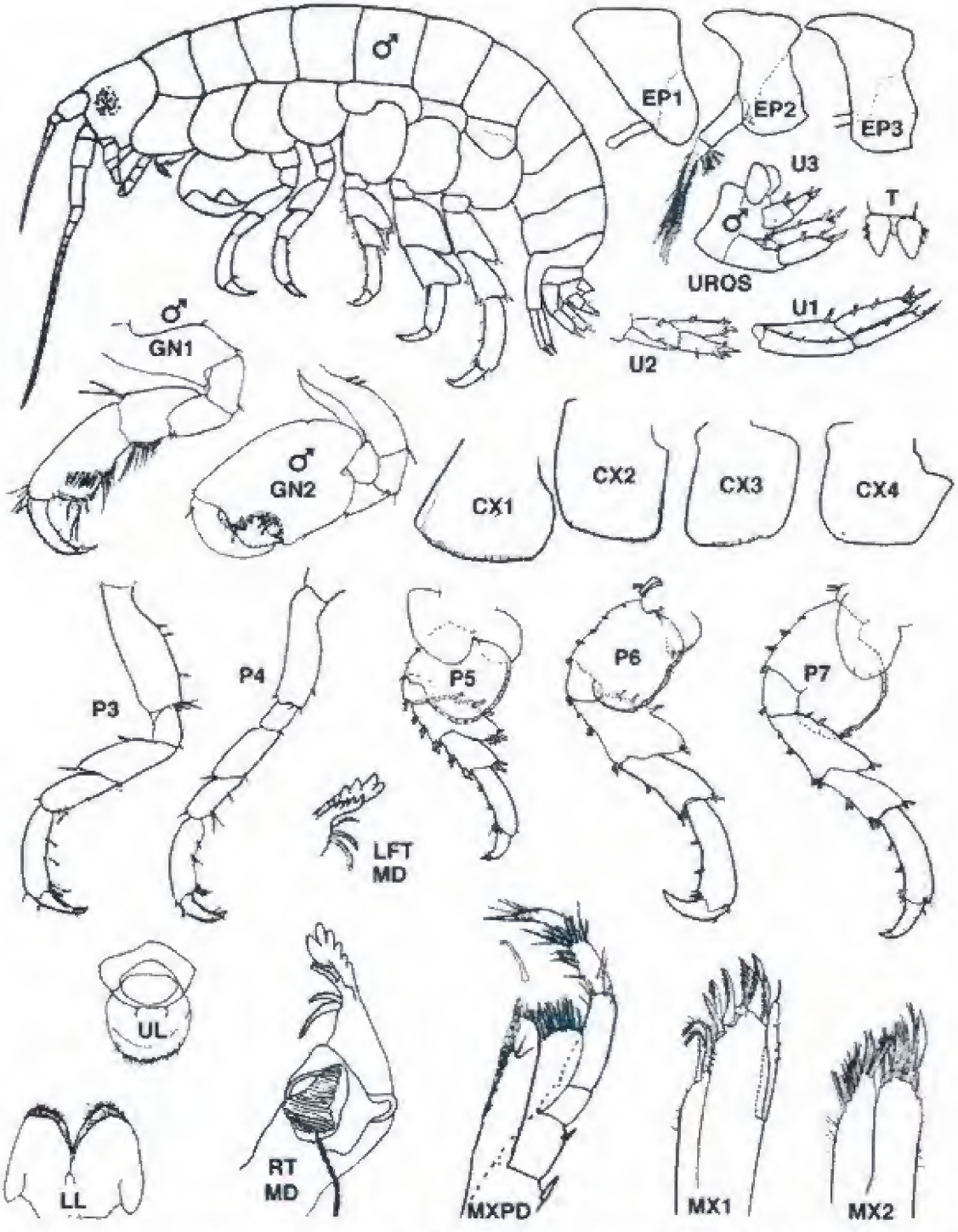

Fig. 45. *Lelehua ishigakiensis* (Hirayama, 1980). Male (4.0 mm). Ishigaki I. Okinawa, Japan.

pod 2 (♂); strong distal peduncular spine of uropod 1; elongate telson lobes; and lack of distinctive posterior marginal cusps on coxae 1-3.

Hyale Rathke sens. str.

Hyale Rathke, 1837: 377.
Hyale (part):Stebbing 1906: 559;—Chevreux & Fage 1925: 280;—Gurjanova 1951: 816;—Bulycheva 1957: 83;—Lincoln 1979: 230;—Krapp-Schickel 1993: 728;—Barnard & Karaman 1991: 367.
non *Nicea* Nicolet, 1849.

Type species: *Hyale pontica* Rathke 1837, present designation.

Species: *Hyale pontica* Rathke, 1837; Krapp-Schickel & Bousfield 2002: 3, figs. 1, 2; *H. lubbockiana* Bate, 1856; Krapp-Schickel & Bousfield 2002: 7, figs. 3,4,5 *H. michelini* Krapp-Schickel & Bousfield, 2002:10,

figs. 6, 7; *Hyale* species Krapp-Schickel & Bousfield, 2002: 12, fig. 8 (Bermuda).

Diagnosis: Body smooth, or segments may be weakly imbricated or weakly mid-dorsally carinate. Eye ovate. Antennae short, slender, subequal. Antenna 2, peduncle not incrassate; flagellum not elongate.

Mandible, left lacinia 5-5 1/2 dentate, spine row with 3-5 blades. Maxilla 1, palp 1-segmented; outer plate, apical spine-teeth tall. Maxilliped, inner plate tall; palp normal, segment 3 short, medium thick; dactyl small, not falcate, unguis regular to elongate.

Coxae 2 and 3 with prominent sharp posterior marginal cusp, lacking in coxae 1 and 4. Coxa 5 anterolobate.

Gnathopods sexually dimorphic. Gnathopod 1 (♂), propodal palm short, variously overhung by simple dactyl; carpal lobe narrow; propod with mediofacial guiding (bracing) spine; dactyl simple. Gnathopod 2 (♂), basis with strong hydrodynamic lobe; carpal lobe lacking; propod large, narrowing distally, palm with slight hinge tooth. Gnathopods (♀) normal; carpal lobes shallow; gnathopod 2 similar to gnathopod 1 but larger,with stronger basal hydrodynamic lobe.

Peraeopods short, stout; bases expanded, posterior margins crenulate, hind margins of peraeopods 5 and 6 with weak surge seta and notch. Peraeopod 5, segment 4 short, broad; segment 5 often short; segment 6 with single large striated subterminal anterodistal clasping (locking) spine, and 1-2 small accessory spines; dactyl large, smooth, anterior marginal seta small.

Epimeral plates 1-3 regular, 3 not produced. Pleopods regular, natatory. Uropods 1 and 2, peduncle and rami short, thick. Uropod 1 lacking distal peduncular spines; rami with medium apical and marginal spines. Uropod 3 short, thick, uniramous; ramus shorter than peduncle, with apical spines only.

Telson broad, lobes slightly longer than broad, margins weakly setose.

Coxal gills small, rounded, largest on peraeopod 5. Female: Brood plates moderately broadened, apices rounded; marginal setae medium-long, curl-tipped. Peraeon 2, preamplexing notch large, rectangular, lacking unguisial groove, with small locking slit above anterior margin of notch.

Distributional Ecology: Open surf coasts of the Mediterranean and Black Seas, and the Northeastern Atlantic, including Great Britain and Norway; also Bermuda; clinging to algae and other substrata, LW level and subtidally to 50 m.

Remarks: Species of *Hyale* sens. str. differ considerably from those of *Apohyale* n. g. (p. 104) in character states of morphology, behaviour, and ecology. According to Sars (1890), *H. lubbockiana* does not saltate in air, unlike *A. nilssoni* and other species of genus *Apohyale*. Mature females of *Hyale* possess regularly rounded brood plates with longish marginal hooked setae (Fig.11F), whereas those of *Apohyale* have very broad, apically acute brood plates with numerous short marginal hook-tipped setae (Fig. 12E).

Species of *Hyale* are apparently uniquely adapted to a life style in strongly lotic waters such as the surf zone of open coasts. Thus, the tip of the large propodal median facial guiding spine (♂) appears to fit into a locking slit on peraeon 2 (♀), thereby enhancing the grip of the gnathopod when the dactyl closes on the preamplexing notch. In apparent homoplasious manner, the preamplexing mechanism within genus *Hyale* resembles that of some species within the North Pacific genus *Allorchestes* (e.g., *A. bellabella* Barnard, family Hyalellidae).

Hyale pontica bears some similarity to *Micropythia carinata* (Bate, 1862) in form of mouthparts (esp. weak distal palp segments and elongate unguis), cusps on posterior mar-gins of coxae 2 &3, lacking on coxae 1 and 4; peraeopods 5-7 with strongly crenulate hind margins of bases, and short broad segments 4 & 5, short uropod 3, and form of brood plates.

Hyale lubbockiana (Bate)
(Figs. 46, 47)

Hyale lubbockiana Bate, 1856: 57, t. 17, fig. 7; Sars, 1890: 27, pl. 11, fig. 2;—Krapp-Schickel & Bousfield 2002: 7, figs. 3, 4, 5.
Hyale pontica Lincoln 1979: 236, figs. 109e-j;—Barnard & Karaman, 1991: 370.

Material Examined:
Port Erin, Isle of Man, in alga at LW, D.I. Williamson coll. March, 1955 - ♂ (7.5 mm) (slide mount)(**fig'd.**), CMNC 1983-1525; ♀ ov. (4.5 mm) (slide mount) (**fig'd.**); CMN collections.

Diagnosis: Like *Hyale pontica* in having slightly setose flagellum of antenna 2, strongly pointed cusp on the posterior margin of coxae 2 and 3, large hydrodynamic lobe on the basis of gnathopod 2 (♂), strongly crenulate hind margins of bases of peraeopods 5-7, single large clasping spine on the distal margin of segment 6 of peraeopods 3-7, and a short blunt uropod 3 that lacks

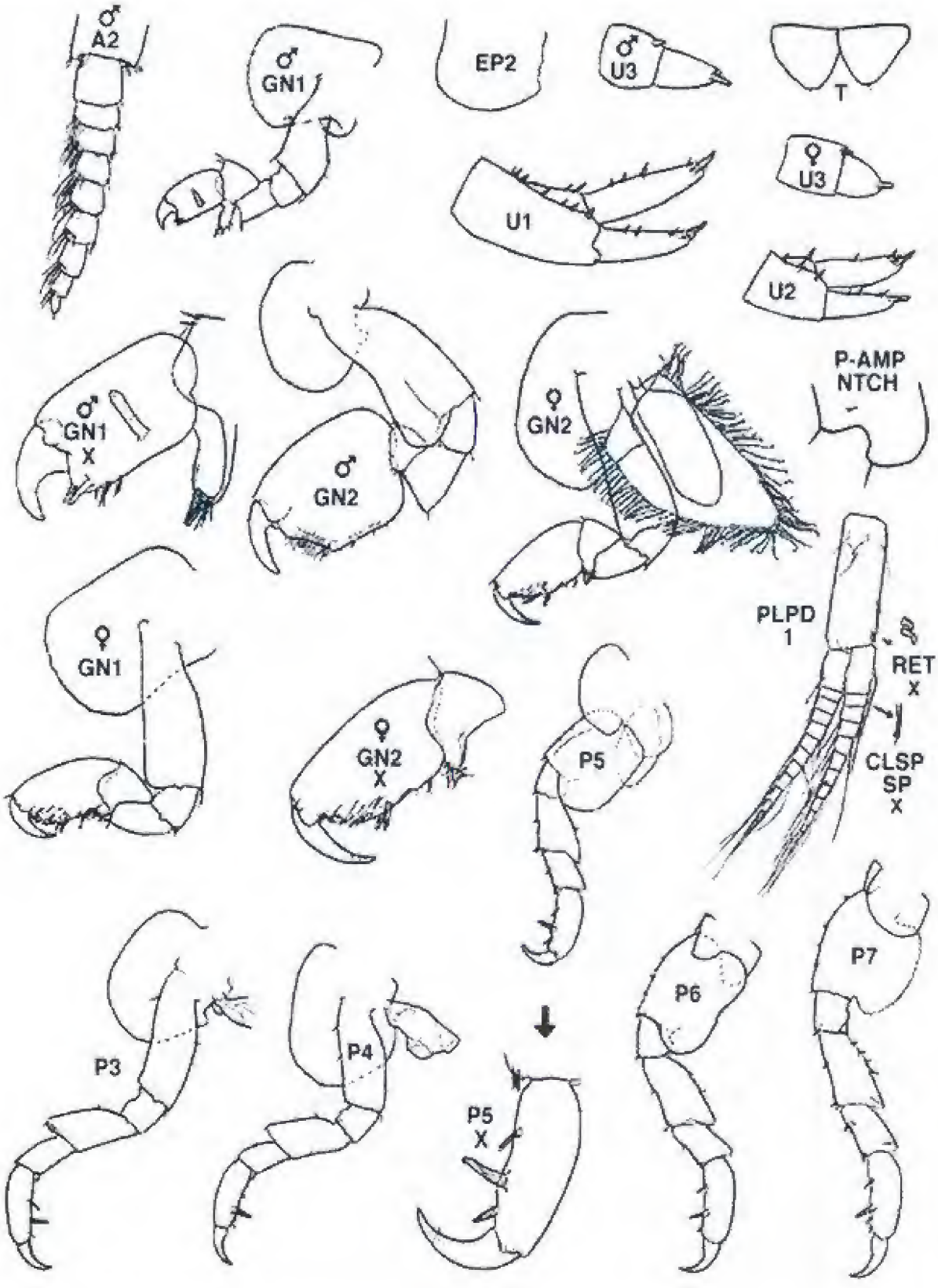

Fig. 46. *Hyale lubbockiana* (Bate, 1856). Male (7.5 mm); female ov (4.5 mm). Port Erin, Isle of Man, Irish Sea.

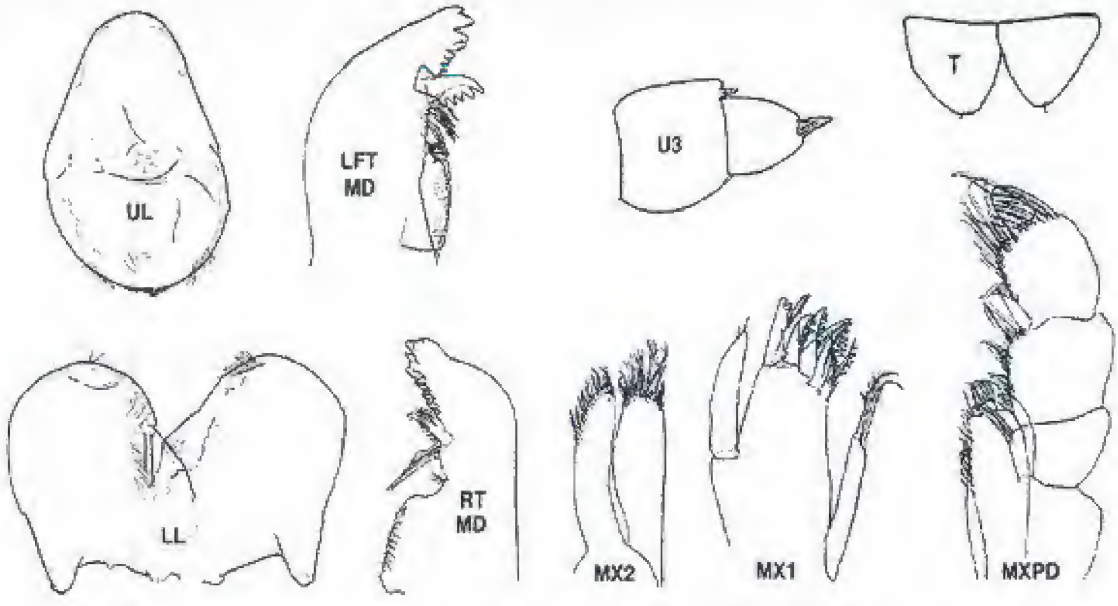

Fig. 47. *Hyale lubbockiana* Bate, 1856. Male (7.5 mm); female ov (6.0 mm). Port Erin, Isle of Man. Irish Sea.

pronounced distal spines on the peduncle of uropod 1.

Hyale lubbockiana differs from *H. pontica* in the normally unmodified condition of the dactyl of the maxilliped palp, and the vertical position of the large medio-facial spine of the propod of gnathopod 1 (♂). In addition, segment 5 of peraeopods 5-6 is short (width nearly equal to length), and the apical margins of the telson lobes are unarmed.

Distributional Ecology: Along exposed coasts of the temperate North Atlantic region, western France and the Irish Sea,to northern Norway, among algae at LW.

Remarks: This species has been recorded previously only from open coasts of the northeastern Atlantic region. Although the genus *Hyale* Rathke sens. str.does not occur in the North Pacific region, the present CMN material from the Irish Sea illustrates character states of the type genus required for comparison with the several new genera proposed herein. The figures also compare closely with those of *H. lubbockiana* from northern Norway figured by Krapp-Schickel & Bousfield (2002). They are less closely similar, however, to those of Sars (1890) in which a preamplexing notch is lacking (mature ♀), or to those of Lincoln (1979) in which the propod of gnathopod 1 (mature ♂) lacks a medio-facial guiding spine, and the mouthparts are not detailed.

Material from the Mediterranean, referred to *H. pontica*, but with character states similar to those of *H. lubbockiana* (e.g., Chevreux & Fage, 1925; Giovannini, 1965) are described elsewhere as *H. michelini* Krapp-Schickel & Bousfield, 2002.

Parhyale Stebbing

Parhyale Stebbing, 1897: 27;—Stebbing 1906: 556;—Shoemaker 1956: 345.
Parhyale (part) Bulycheva 1957: 78 ;—Krapp-Schickel 1974: 326;—Barnard 1979: 120 (key);—Arresti 1989: 112;—Krapp-Schickel 1993: 754;—Ishimaru1994: 69.
Hyaloides Schellenberg, 1939: 126.

Type species: *Parhyale fasciger* Stebbing,1897 monotypy.

Species: *Parhyale aquilina* (Costa, 1853) (see also Chevreux & Fage 1925 (as *Allorchestes*); *P. basrensis* Salman, 1986; *P. eburnea* Krapp-Schickel, 1974 (also Krapp-Schickel 1993); *P. fascigera* Stebbing, 1897 (also Shoemaker 1956); *P. hawaiensis* (Dana, 1853)(= *Allorchestes chelonites* Oliveira, 1953: fide Young, 1998); *P. inyacka* K. H. Barnard, 1916 (Griffiths 1973; Barnard 1979); *P. iwasai* Shoemaker, 1956 (=*Hyale gracilis* Iwasa, 1939); *P. multispinosa* Stock, 1987; *P. penicillata* Shoemaker,1956 (Krapp-Schickel 1974; J. L. Barnard 1979); *P. plumicornis* (Heller, 1866) (Krapp-Schickel 1974).

Diagnosis: Body smooth, small to medium. Eye medium, vertically lenticular or almond-shaped. Antenna 1, peduncular segments regular, not shortened. An-

tenna 2, peduncular segments 4 & 5 strong; flagellum elongate, usually bare; if setose (♂), setae also on peduncular segment 4 and 5.

Mandible, left lacinia 5-dentate. Maxilla 1, palp 1-segmented (often with middle constriction and appearing subequally 2-segmented), outer segment little exceeding base of apical spines of outer plate. Maxilla 2, inner plate slender, with 1-2 proximal marginal plumose seta; inner plate with pectinate apical setae. Maxilliped palp medium thick, falciform; segment 2 inner margin straight; dactyl slender, curved, nail short.

Coxae 1-4 with distinct posterior marginal shelf, cusp variously developed. Coxa 1 broadened distally. Coxa 4 with cusp in middle of posterior marginal excavation. Coxa 5 aequi-or slightly anterolobate. Coxal gills saclike, slightly largest on peraeopod 6.

Gnathopod 1 (♂) basis and ischium lacking hydrodynamic lobe; carpal lobe broad; propod short, deep, with lower marginal setal cluster; paired spines at posterodistal angle unequal, separated; dactyl simple, inflated to aquiline. Gnathopod 2 (♂), basis with small acute hydrodynamic lobe; carpal lobe weak or lacking; propod subrect-angular, palm smooth, oblique; dactyl stout.

Peraeopods 3-7 slender, weakly spinose; segments not shortened; dactyls short, curved, with inner marginal seta. Peraeopods 5-7, hind margin of basis with notch and surge seta . Peraeopod 6, basis narrower than 5 and 7.

Epimeral plates regular , not produced. Pleopods regular, strong. Uropod 1, rami weakly spinose, peduncle typically with distolateral spine; uropods 1 and 2, rami typically subequal, with marginal spines. Uropod 3 biramous, outer ramus with apical spines only; inner ramus small, usually distinct , occasionally partly fused to peduncle outer ramus short, apically spinose.

Telson lobes not elongate, margins smooth or with small apical seta.

Female: Gnathopods 1 and 2 slightly differing in size and form; basis with small subacute hydrodynamic lobe. Brood lamellae medium broad, elongate,with medium length marginal setae and sharply rounded apex. Preamplexing notch a simple anterodistal marginal excavation, lacking unguisial groove.

Distributional Ecology: Cosmopolitan-tropical and warm-temperate; intertidal and littoral marine. Although two species occur in the warm-temperate and tropical western and central North Pacific, none has yet been recorded from the eastern North Pacific.

Remarks: *Parhyale iwasai* Shoemaker, 1956, was originally described and figured as *Hyale gracilis* Iwasa, 1939. Iwasa made no mention of a minute inner ramus on uropod 3, diagnostic of genus *Parhyale*. The authors agree with the conclusions of Shoemaker (1956), Bulycheva (1957), Barnard & Karaman (1991). Thus, despite Iwasa's orginal descriptive oversight, on the basis of all other generic level character states, especially the process on the posterior marginal excavation of coxa 4, the species is now correctly assigned.

Parhyale hawaiiensis (Dana, 1853)
(Fig. 48)

Remarks: The species occurs in the southern and western peripheries of the North Pacific study region as well as widespread along tropical oceanic coastlines world-wide. Taxonomic features are illustrated here (Fig. 48) for direct comparison with species of the north Pacific genus *Parallorchestes* (Table II) with which it has been synonomized by several authors (e.g., Stebbing 1906; Bulycheva 1957; Stock 1987).

Especially distinctiveof *Parhyale* are the following character states: (1) maxilla 1, palp 1-segmented; (2) gnathopods 1 and 2 (both sexes) bases with small hydrodynamic lobes; (3) gnathopod 1 (male), dactyl aquiline in form; (4) gnathopod 2 (male), carpal lobe very small or lacking; (5) peraeopod 3-7, dactyls small, each with distinct anterior marginal seta; (6) coxa 4 with broad posterior marginal cusp; and (7) peraeon 2 (mature female) with weakly incised preamplexing notch, lacking unguisial groove.

Parhyale fascigera Stebbing

Parhyale fascigera Stebbing, 1897: 26-28, pl. 6;—Shoemaker 1956: 346-350, figs. 1, 2a-f;—Barnard 1979: 123.

Remarks: The figures of Shoemaker (1956) demonstrate some variation in form and armature of gnathopod 1 and peraeopod 7 of mature males of *Parhyale fascigera* Stebbing from the eastern Caribbean region. Thus, in material from St. Croix, the medial facial spine of the propod was distinctly enlarged and displaced from the posterodistal angle, relative to the condition in similar sized males from Martinique. However, Barnard (1979), who re-examined the original material on deposit in the USNM, was satisfied of their overall conspecificity.

Key to World Species of *Parhyale* Stebbing

1. Antenna 2, flagellum short (12-22 segments); uropod 1, peduncular distolateral spine weak, little larger than adjacent spines; uropod 3, outer ramus short, << peduncle ..... 2.
Antenna 2, flagellum long (>25 segments); uropod 1, peduncular distolateral spine strong, prominent; uropod 3, ramus medium to long, length subequal to peduncle ..... 3.

2. Antenna 2, flagellum 20-22 segmented; gnathopod 2 (♂) dactyl inflated (aquilinated); epimeral plate 3, hind corner acute; uropod 2, outer ramus 1-2 marginal spines ..... *P. aquilina* (Costa)
Character states otherwise ..... *P. eburnea* (Krapp-Schickel)

3. Antenna 2 (♂), peduncular segments 4 & 5 setose; gnathopod 2, carpal lobe strong ..... 4.
Antenna 2 (♂), peduncular segments 4 & 5 bare; gnathopod 2, carpal lobe weak or lacking ..... 5.

4. Peraeopod 7, segment 6, anterior margin with 5-6 spine groups; epimeral plate 3, hind corner acute ..... *P. plumicornis* (Heller)
Peraeopod 7, segment 6, anterior margin with 2-3 spine groups; epimeral plate 3, hind corner squared ..... *P. penicillata* Shoemaker

5. Gnathopod 2 (mature ♂), carpal lobe present, small; gnathopod 1, medial spine at posterodistal angle of propod distinctly enlarged and displaced; dactyl strongly inflated ..... *P. fascigera* Stebbing (p. 97)
Gnathopod 2 (mature ♂), carpal lobe lacking; gnathopod 1, medial spine little enlarged or displaced from other posterodistal propodal spine; dactyl slightly inflated. ..... 6.

6. Uropod 1, outer ramus with single marginal spine; uropod 2, outer ramus lacking marginal spines; peraeopod 7, segment 6, anterior margin with 1-2 spines ..... *P. iwasai* Shoemaker.
Uropod 1, outer ramus with 2-4 marginal spines; uropod 2, outer ramus with 2-3 marginal spines; peraeopod 7, segment 6 with 3-5 marginal spines ..... 7.

7. Maxilliped palp (♂), segment 3 with strong distal setal cluster; uropod 3, ramus strong, with many distal and marginal spines ..... *P. inyacka* K. H. Barnard
Maxilliped palp (♂) segment 3 with regular distal setation; uropod 3, ramus ordinary ..... 8.

8. Peraeopods 6 & 7, segment 6, posterior margin with 6-7 spine groups; uropod 1, outer ramus with 6 spine groups ..... P. *multispinosa* Stock
Peraeopods 6 & 7, segment 6, posterior margin with 3-4 spine groups; uropod 1, outer ramus with 2-3 spine groups ..... *P. hawaiensis* (Dana) (p. 97)

Other species of *Parhyale*.

CMN collections contain moderately extensive material of males and females of genus *Parhyale*, from widely scattered localities, mainly in the Indo Pacific region, but also from the North Atlantic, including Bermuda. Duplicate material of B.M. Kunkel (1910), then identified as "*Hyale pontica*", permits diagnosis of character states of females including the brood plates and preamplexing notch. All hyalid species described and attributed to genus *Hyale* by Kunkel (loc. cit.) have proven identical with *Parhyale hawaiiensis* (Dana)(Fig. 48), an intertidal species of that oceanic island (Johnson 1986; Krapp-Schickel & Bousfield 2002).

Dr. Takehiko Hiwatari is currently describing markedly differing species of *Parhyale* from Japan and the Philippine Islands. However, the phyletic significance of character state differences has not yet been determined..

***Ptilohyale* n. g.**

Hyale (part) Barnard 1969a: 469;—Barnard 1979: 98;—Barnard & Karaman 1991: 367;—Ishimaru 1994: 67.
Parhyale (part) Stebbing 1906: 559;—Krapp-Schickel 1993: 754.
Allorchestes (part) Bulycheva 1957:111.
non *Parhyale* Stock 1987: 167.

Type Species: *Allorchestes plumulosa* Stimpson,1857 (present designation)

Species:
Ptilohyale barbicornis Hiwatari & Kajihara, 1981a (= *H. plumicornis:* identifications of Iwasa 1939; Nagata 1965); *P. crassicorne* (Haswell,1879), (Chilton 1885) (J. L. Barnard 1974) (= *H. coogensis* Chilton, 1885); *P.*

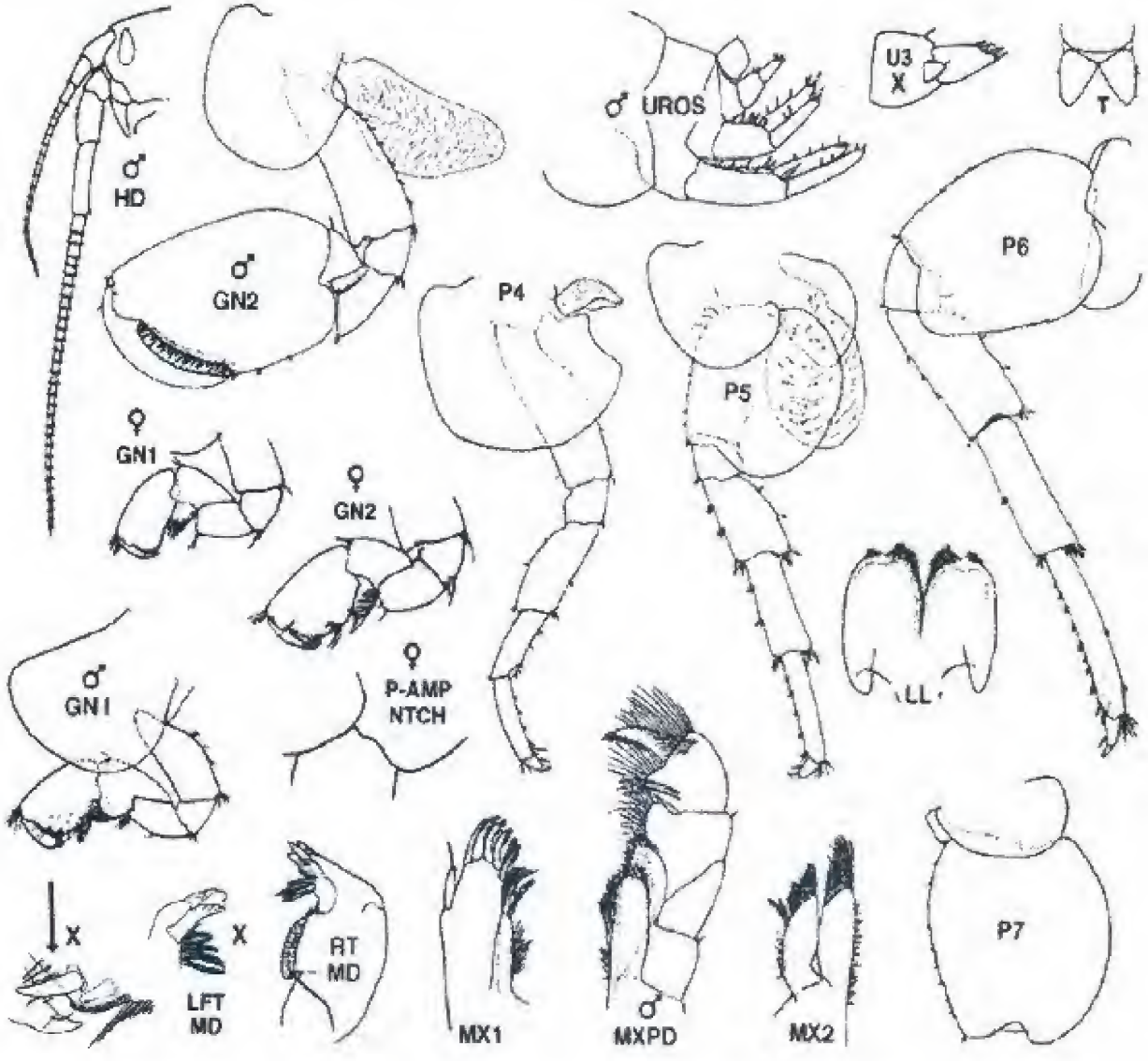

Fig. 48. *Parhyale hawaiiensis* (Dana, 1853). Male (12 mm). Tortugas, Florida. (after Shoemaker 1956). Female ov (~7 mm). Mauritius. (CMN collections).

eburnea (Krapp-Schickel, 1974), 1993; *P. explorator* (Arresti, 1989); *P. iole* (J. L. Barnard, 1970); *P. littoralis* (Stimpson, 1853); *P. plumicornis* (Heller, 1866) (Krapp-Schickel 1974); *P. plumulosa* (Stimpson, 1857); *P. ptiloceros* (Derzhavin, 1937); *?P. tristanensis* (Macnae, 1953); *P. barnardi* Chevreux, 1925); *Ptilohyale* sp. Griffiths, 1976 (not = *P. plumulosa* Stimpson, 1857).

Diagnosis: Body medium, smooth. Eyes lenticular, vertical, medium. Antenna 1 medium, peduncular segments not shortened, flagellum slender. Antenna 2, peduncle 4 short; flagellum short to medium (<20-segmented), posteromedial margin of flagellum and peduncular segment 5 strongly plumose-setose.

Mandibular left lacinia 5-dentate (rarely 6), spine row with 3-6 blades. Maxilla 1, palp stout, 1-segmented, reaching base of apical spines of outer plate. Maxilla 2, inner plate with 1-2 inner marginal plumose setae. Maxilliped, inner plate relatively short; outer plate distally obtuse; palp, segment 2 not broader than long; dactyl slender, unguis short.

Coxae 1-4 rounded below, with posterior marginal cusps. Coxa 1 slightly distally broadened. Coxa 5 anterolobate; coxae 6 and 7 posterolobate. Coxal gills slender-subovate, sac-like, largest on coxa 6.

Gnathopod 1 (♂) larger and slightly different in form to female; basis lacking hydrodynamic lobe; carpal lobe distinct, relatively broad; propod hachet-shaped broadening distally, lacking mediofacial guiding spine; palm distinct, oblique, dactyl simple. Gnathopod 2 (♂) powerfully subchelate, regular; basis with medium hydrodynamic lobe; carpal lobe small, thin, evanes-

cent; propod subrectangular to subovate, narrowing distally, palm short, oblique, not incised or toothed; dactyl regular.

Peraeopods 3-7 slender, regular; dactyls small, with distinct but weak inner marginal seta. Peraeopods 5-7, bases medium broad, rounded hind margin not strongly crenulate, lacking surge seta and notch; segments 4-6 slender, not broadened; marginal spines weak, not striated, clasping spine weak or lacking.

Epimeral plates relatively broad, margins weakly armed, hind corner not produced. Pleopods well developed, rami normal. Uropod 1, peduncle longer than rami, with strong distomedial spine; rami with marginal spines, and medium apical spines. Uropod 2, rami subequal, with marginal spines. Uropod 3 short, peduncle with lateral setal row and postero-dstal spine; inner ramus variously fused to peduncle; outer ramus subequal to peduncle, with stout apical spines .

Telson lobes triangular, longer than wide, margins smooth.

Female: Gnathopod 2 , propod similar to, but larger and deeper than in gnathopod 1. Brood plate large, medium broad, apically acute; marginal setae short, hook-tipped, numerous. Preamplexing notch shallow, with short to medium unguisial groove; posteroventral lobe of peraeon 2 large, anterior margin convex.

Distributional Ecology: Low intertidal of estuaries, and subtidally on *Poccilopora* sp., to depths of 30 m. (Barnard 1970); Atlantic-Mediterranean region; North and central Pacific to Japan, south to Australia..

Etymology: From the Greek root "*ptilo*" meaning downy plumage + *Hyale*, alluding to the downy or finely setose posterior margin of antena 2 in males and most females.

Remarks: The *Ptilohyale* generic group is remote from *Hyale*, type genus of family Hyalidae. Especially distinctive character states are: (1) heavily plumose (finely brush-setose) antenna 2 (both sexes); (2) lack of a guiding spine on the medial face of the propod of gnathopod 1 (♂); (3) variously developed carpal lobe of gnathopod 2 (♂); (4) distomedial spine on the peduncle of uropod 1; (5) inner ramus of uropod 3 variously fused to the peduncle. Species of *Ptilohyale* are mainly brackish and estuarine, whereas those of *Hyale* frequent high salinity surf-coast waters.

A number of undescribed species of *Ptilohyale* from New Zealand and South America (Cape Horn region) have been noted in CMN collections.

Ptilohyale plumulosa (Stimpson)
(Fig. 49)

Allorchestes plumulosa Stimpson, 1857: 519;—Stebbing 1906: 585.
Hyale plumulosus Thorsteinson 1941: 55, pl. 1, figs. 10-15;
Hyale plumulosa Barnard 1969b: 138;—Barnard 1979: 114:—Austin 1985: 595;—Staude 1987: 379;—Barnard & Karaman 1991: 370.
Plumulohyale plumulosa Bousfield 1981: 80, fig. 9;—Bousfield 2001a: 104.
non: *Hyale plumulosa* Bousfield 1973: 155, Pl. XLIV, fig. 2.(Atlantic); Griffiths 1976: 76, fig. 51B (S. Africa).

Material Examined: 69 lots containing ~360 specimens, from SE Alaska to Oregon & S. California. (Numbers of specimens at each station in parentheses. Stations data provided in Bousfield 1958, 1963, 1968; Bousfield & McAllister 1962; Bousfield & Jarrett 1981).

ALASKA
Southeastern Alaska: ELB Stn, 1961: A164, NW side Hogan I., Imperial Passage, LW-HW tide pools, - 1 ♂, 1 im.
ELB Stns, 1980: S19B2 (1♂ , 2 ♀♀); S20B1 (6♂♂, 1 ♀).

BRITISH COLUMBIA
Queen Charlotte Islands: ELB Stns, 1957: E8 (10), E9 (3), W14a (10), E24 (6), W5a (11)
North Central Coast: ELB Stns., 1964: H2 (2), H4 (3), H6 (1), H11 (3), H16 (2), H33 (51), H46 (10), H48 (2), H51 (10).
South Central Coast: ELB Stns, 1955: M1a (1), M2 (26), M3 (64), M5 (1), M11 (5).
ELB Stns, 1976: B9 (1).
North Vancouver Island: ELB Stns, 1959: N13 (1), N23 (6), V4a (1), V20 (1).
Southern Vancouver Island: 1955, ELB Stns: F1 (8), G2 (6), G11 (13), G21 (5), P2 (10).
1964, ELB Stn: H44 (5)
1970, ELB Stns: P708 (2), P710 (2), P712 (4), P719 (18).
1975, ELB Stns: P6 (15), P7 (1), P16 (24) P19 (3)
1976, ELB Stns: B3a, Diana I., Trevor Channel beach, S. side (48°50'12"N, 125°11'W, under stones, LW, June 26 - **Neotype** specimen: 1 ♂ (8.5 mm) (slide mount) (**fig'd**), CMNC 1983-1527; **Voucher** specimens: 1 ♀ ov (7.0 mm)(slide mount) (**fig'd**), 5♂♂, 7♀♀ ov., CMNC 2002-0076; B13 (14), B28 (20).
1977, ELB Stns: B4 (3), B12 (5).
Additional B. C. Localities (CMN collns.): Hecate Strait, from stomach contents of sole, J. Madill, 1983 - 1 spm.; Swanson Bay, C. D. Levings coll., 1973 - 1 spm; Rocky Pt., C. Lobban coll., 1971 - 1 ♂; Saltspring I., R. Long coll., 1977 - 2 spms.; Anthony I., Q. C. I., G C Carl coll., 1958 - 1 ♂; Trable I., D.V. Ellis coll., 1975 - 3 spms.

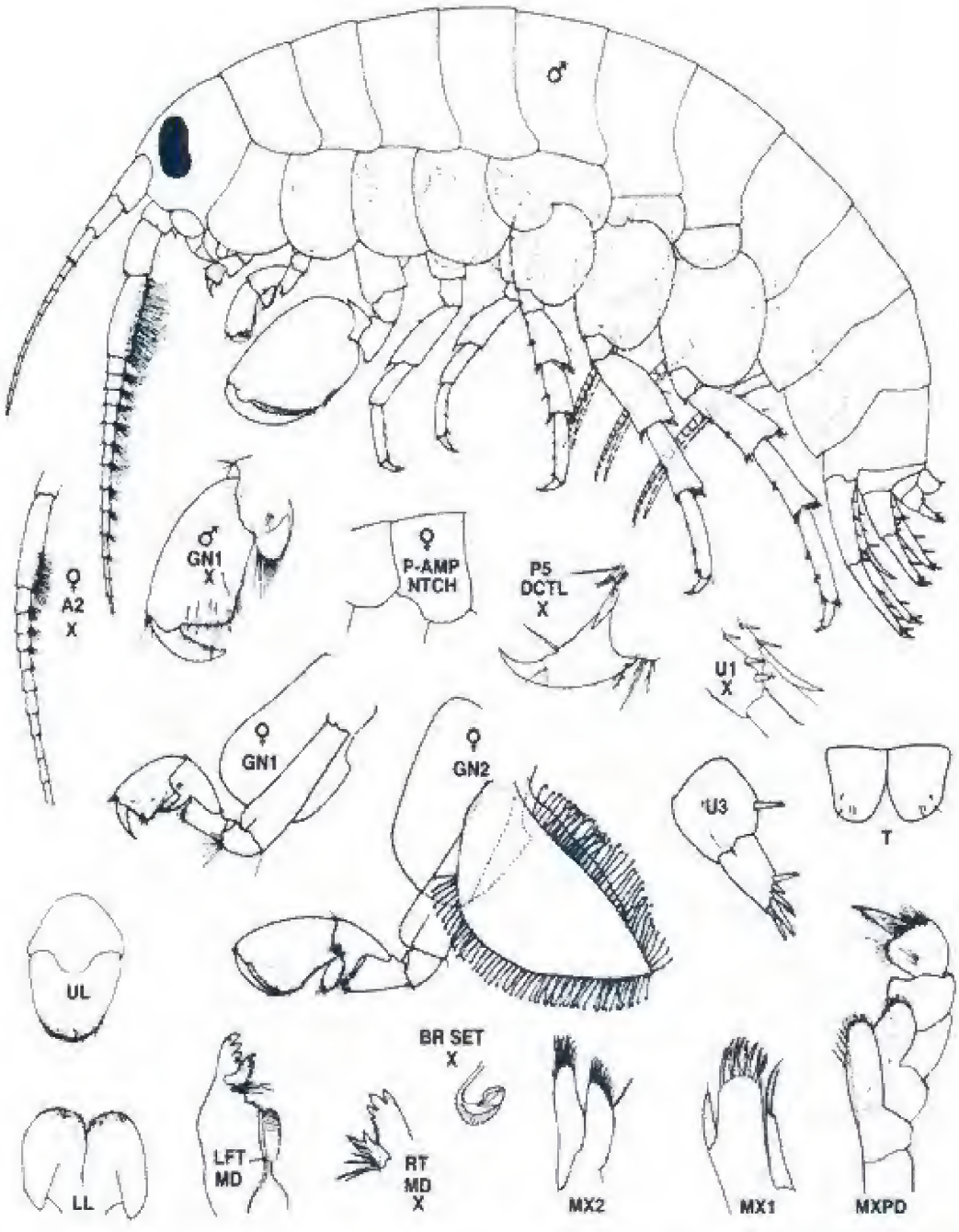

Fig. 49. *Ptilohyale plumulosa* (Stimpson, 1857). Male (8.0 mm); ELB Stn.B3, Diana I., Trevor Channel,B.C.; female ov (7.5 mm). ELB Stn. B4, Piper's Lagoon,Vancouver I, B. C.

WASHINGTON-OREGON
ELB Stn, 1955: M11 (8).
ELB Stns, July-Aug., 1966: W3 (2), W5 (1), W8 (1), W9 (20), W15 (9), W29 (11), W 31 (4), W36 (1), W40 (8), W47 (4), W53 (7), W65 (11).

CALIFORNIA
ELB Stn., 1959: C3, Eureka, CA, LW - 18 specimens.
Other Material (CMN collns.): Mission Bay, San Diego, C. D. Clark coll, 1956 - 1 specimen.

MEXICO
Turtle Bay, Baja California, W. L. Klawe coll., 1956 - 26 specimens.

Diagnosis: Male (11.0 mm): Body medium large, smooth. Eye broadly reniform. Antenna 1, peduncular segment not shortened; flagellum 10-12 segmented. Antenna 2,flagellum 12-13 segmented, proximal 10 segments and peduncular segment 5 with dense posterior marginal tufts of medium long plumose seta.

KEY TO NORTH PACIFIC & WORLD SPECIES OF *PTILOHYALE*

1. Uropod 1, outer ramus with 4-5 marginal spines; uropod 2, rami unequal in length; uropod 3, ramus with 7-8 apical spines ..... *P. explorator* Arresti
   Uropod 1, outer ramus with 3 (2) marginal spines; uropod 2, rami subequal in length; uropod 3, ramus with 5-6 apical spines ..... 2.

2. Coxa 5, posterior lobe distinctly smaller than anterior lobe; gnathopod1 (male), basis lacking distinct antero-distal lobe; peraeopod 5, basis narrow. ..... *P. littoralis* (Stimpson) (p. 103)
   Coxa 5, lobes subequal or hind lobe slightly smaller; Gn1, basis lobate; peraeopod 5, basis broadly rounded as in peraeopods 6 & 7. ..... 3.

3. Peraeopod 5 basis broad; uropod 3, ramus with 5 apical spines ..... 4.
   Peraeopod 5, basis narrower than in P6 & &; uropod 3, ramus with 6 apical spines ..... 5.

4. Antenna 2 (♂), flagellar segments densely setose; gnathopod 2, carpal lobe evanescent; telson lobes acute . . . . *P. crassicorne* Haswell
   Antenna 2(♂), flagellar segments normally setose; gnathopod 2, carpal lobe present; telson lobes apically rounded ..... *P. plumulosa* Stimpson (p. 100)

5. Antenna 2 (♂), flagellar segments 1-8 densely setose ..... *P. iole* (Barnard)
   Antenna 2 (♂), flagellar segments moderately setose ..... 6.

6. Gnathopods 1 & 2 (♀), propods slender (Russian coast) ..... *P. ptiloceros* (Derzhavin)
   Gnathopods 1 & 2 (♀). propods broadening distally; (Japan) . . . *P. barbicornis* (Hiwatari & Kajihara) (p. 104)

Mandibule, spine row with 4 blades. Maxilla 1, palp narrowing, barely reaching base of outer plate spines. Maxilliped, dactyl nearly straight, not longer than segment 3.

Coxae 1-4, hind marginal cusps bluntly rounded. Coxa 5, lobes subequal or hind lobe slightly smaller. Coxal gills relatively large, broadly sac-like.

Gnathopod 1, basis weakly lobate;carpal lobe short, broad, lower margin with 12-14 comb satae; propod slightly broadening distally, palm straight,nearly vertical, hind margin distally lined with short setae; dactyl not overlapping palm. Gnathopod 2 with medium h.-d. lobe; carpal lobe vestigial; propod large, subrectangular, palm oblique gently convex, evenly lined with short spines,

Peraeopods 3-4 relatively slender, margins weakly spinose, dactyls short, inner margin very weakly castellate. Peraeopods 5-7 increasing in length, bases broadly rounded; segment 5 slender, not shortened.

Epimeral plates 1-3 hind corners nearly square. Uropod 1, peduncular distomedial spine elongate, length 1/2 inner ramus; rami slender, longer than peduncle with 1-3 marginal spines. Uropod 2, outer ramus slightly the shorter. Uropod 3 short; inner ramus fused to peduncle; outer ramus, apex oblique, with 5-6 apical spines. Telson lobes slightly longer than wide, apices rounded.

Female ov (8.0 mm). Antenna 2, proximal 4-5 flagellar segments and posterodistal margin of peduncular segment 5 with clusters of short plumose setae. Gnathopod 1 distinctly larger than 2, propods broadening distally. Brood plate (gnathopod 2) relatively short, broad, apex acute, marginal setae medium. Pre-amplexing notch shallow, obtuse; unguisial groove short or lacking.

Distributional Ecology: From southeastern Alaska and British Columbia to southern California and Baja California; mainly estuarine, among *Enteromorpha*, other algae, and *Zostera*, and under cobbles, LW level to shallow subtidal.

Remarks: Although *Ptilohyale plumulosa* (Stimpson) and *P. littoralis* (Stimpson) had been synonymized by Bousfield (1973), the Pacific and Atlantic species differ in character states outlined in the key (above). Similarly, the S. African species keyed and figured by Griffiths (1976) differs from "*Hyale plumulosa*" Stimpson and may be an undescribed species.

North American Atlantic species of *Ptilohyale*.

Because of previous confusion in species identity of North American Pacific and Atlantic material here assigned to genus *Ptilohyale* (e.g., Bousfield 1973; Barnard & Karaman 1991), the name *Ptilohyale littoralis* (Stimpson, 1853) is resurrected to encompass

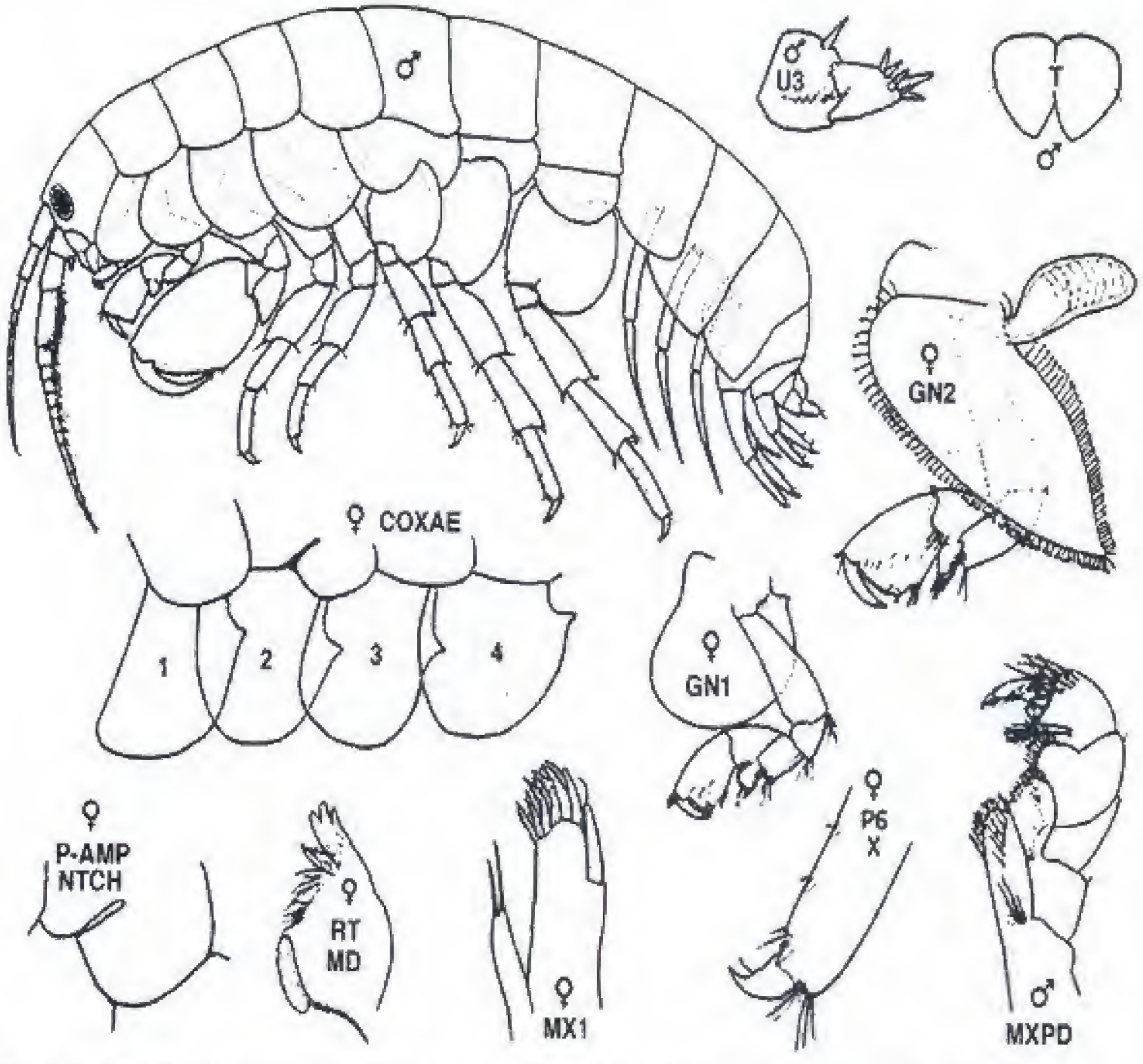

Fig. 50. *Ptilohyale littoralis* (Stimpson, 1853). Male (11 mm). Nobska Pt., Woods Hole, MA (after Bousfield,1973); female ov (8 mm), neotype. Pt. Judith, RI.

the Atlantic species. As the original material of that species cannot be located (lost with many other Stimpson types in the Chicago fire of 1871?), neotype material from the New England region is designated herewith.

Ptilohyale littoralis (Stimpson)
(Fig. 50)

Allorchestes littoralis Stimpson, 1853: 49, t 3, fig. 36; —Smith 1873: 556;—Stebbing 1906: 595;—Miner 1950: 462, pl. 148.

Hyale littoralis Holmes 1905: 472, Pl.3, fig. 2;—Barnard & Karaman 1991: 369.

Hyale prevosti (part) Della Valle 1893: 519.

Hyale plumulosa (Stimpson) Bousfield 1973: 155, pl XLIV.2;—Pollock 1998: 241, fig. 15.120.

Plumulohyale plumulosa (Stimpson) Bousfield 2001a: 104.

Material Examined:

ELB Stn W3, Nobska Pt., Woods Hole, Mass., under cobbles, MW-LW, Sept.1, 1963 - **Neotype** material: ♂ (11.0 mm)(slide mount)(**fig'd**), CMNC 2002-0071; **Voucher** specimens: ♀ ov. (8.0 mm)(slide mount)(**fig'd**), 5 additional specimens, CMNC 2002-0077.

Lewes, Delaware, estuary, July 12, 1977, ELB & class coll. -♂♂, ♀♀, CMN colIns.

Diagnosis: Male: (11.0 mm) Antenna 1, peduncular segments relatively long, thin. Antenna 2 short, flagellum 13-15 segmented; peduncular segment 5 and basal flagellar segments lined posteriorly with relatively short, plumose setae.

Left lacinia 5-dentate, spine row with 3 blades. Maxilla 1 regular. Maxilliped palp stout; dactyl longer than segment 3.

Coxae 1-4, rounded below, hind margins with dis-

tinct cusp. Coxa 5 anterolobate, posterior lobe distinctly smaller than anterior lobe. Coxal gills relatively small, sac-like.

Gnathopod 1, basis and ischium lacking distinct hydrodynamic lobe. Gnathopod 2 regular,basis with small hydrodynamic lobe; carpal lobe small, not protruding; propod large, slightly broadening distally.

Peraeopods 3-7 slender, segments not shortened; dactyls very short; bases broad, hind margins with weak notch and surge seta.

Uropod 1, outer ramus with 3 (2) marginal spines. Uropod 2, rami subequal in length. Uropod 3, ramus with 5-6 apical spines.

Telson lobes medium, apex subacute, margins smooth.

Female ov. (8.0 mm). Gnathopods similar in form. Gnathopod 2, basis with small hydrodynamic lobe; propod distinctly larger than in gnathopod 1. Brood plate (gnathopod 2) large, elongate, narrowing to acute apex, marginal setae relatively short. Preamplexing notch short, squared; unguisial grove medium, oblique; posterodistal lobe of peraeon segment 2 relatively broad and deep, with truncate anterior margin .

Remarks: Bousfield (1973) had synonymized this species with *Hyale plumulosa* (Stimpson, 1857) on superficial morphological similarities. Although the ecology and life styles of *P. littoralis* and *P. plumulosa* are similar, taxonomic differences are significant (see key, p. 102) including the greater degree of development of the posterior marginal cusps of coxae 1-3, the much larger and more distally acute form of the brood lamellae, and smaller size of the marginal setae.

Central and Western Pacific Species of Ptilohyale

The first species of the genus recorded from the western North Pacific was *Allorchestes ptiloceros* Derzhavin, 1937 (see Gurjanova 1951: 823: fig. 576). Bulycheva (1957) synonymized it with the superficially similar Mediterranean species *Allorchestes plumicornis* Heller,1866. However, the Russian Pacific species is proving distinct from the European species as well as from *Ptilohyale barbicornis* Hiwatari & Kajihara, 1981, of Japanese coastal waters.

Ptilohyale plumulosa (Stimpson) resembles *P. ptiloceros* but Derzhavin (1937) does not treat the brood plates, preamplexing notch (♀) or other critical details. Distinctive character states of *P. ptiloceros* include: (1) gnathopod 2 (mature ♂), carpal lobe thin but visible; (2) peraeopods 5-7, bases relatively slender; and (3) uropod 3, outer ramus elongate, the inner ramus partly fused to the peduncle.

Ptilohyale barbicornis (Hiwatari & Kajihara)
(Fig. 51)

Hyale barbicornis Hiwatari & Kasihara, 1981 b: 21, figs. 1-3;—Barnard & Karaman 1991: 369;—Ishimaru 1994. 67.
Allorchestes plumicornis Iwasa 1939: 289, pl.22, figs. 25-26.

Material examined: Near Tokyo, Japan; among mussels along shore, Hiwatari coll. - ♂ (11.6 mm); ♀ ov (9.2 mm), (CMN collections).

Remarks: Although lacking the female preamplexing notch, the excellent figures of *P. barbicornis* provided by Hiwatari and Kasihara (1981b) exhibit nearly all major characteristic states of genus *Ptilohyale*. These include the coxal gills and sexually dimorphic features of antennae and gnathopods not shown in illustrations of North American, Hawaiian, and other world species.

Ptilohyale barbicornis appears similar to *P. ptiloceros* (Derzhavin,1937). However, in a forthcoming paper, Dr. Hiwatari (pers. comm.) expects to demonstrate the taxonomic distinctiveness of *P. ptiloceros* and *P. barbicornis*.

***Apohyale* n. g.**

Hyale (part) Stebbing 1906: 559;—Gurjanova 1951: 816;—Bulycheva 1957: 83;—Barnard 1974: 66;—Barnard 1979: 98;—Barnard & Karaman, 1991: 367.
Hyale grandicornis novaezealandiae group Hurley 1957: 904;—Bousfield 1981: 76.
H. grandicornis complex Barnard 1969b: 136;—Barnard 1979: 114.
Apohyale Bousfield 2001a:104 (nomen nudum).

Type species: *Allorchestes pugettensis* Dana,1853 (author selection).

Species: **Apohyale anceps* (Barnard,1969b); *A. ayeli* (J. L. Barnard, 1955); **A. bassargini* (Derzhavin, 1937); **A. bishopae* (J. L. Barnard, 1955); **A. californica* (J. L. Barnard, 1969b); *A. crassipes* (Heller, 1866)[=*A. gulbenkiani* (Mateus & Mateus, 1962; Ibid, 1965); *A.? diastoma* (K. H. Barnard, 1916); *A. furcata* (Reid,1951); *A. grandicornis* (Kroyer, 1845); **A. hirtipalma* (Dana, 1853); *A. humboldti* (J. L. Barnard, 1979); *A. media* (Dana,1853); *A. minor* (Chevreux & Fage, 1925); *A. novae-zealandiae* (Thomson, 1879); *A. perieri* (Lucas, 1846); *A. prevostii* (Milne Edwards, 1830) [=*A. nilssoni* (Rathke,1843)]; **A. pugettensis* (Dana, 1853); **A. punct-*

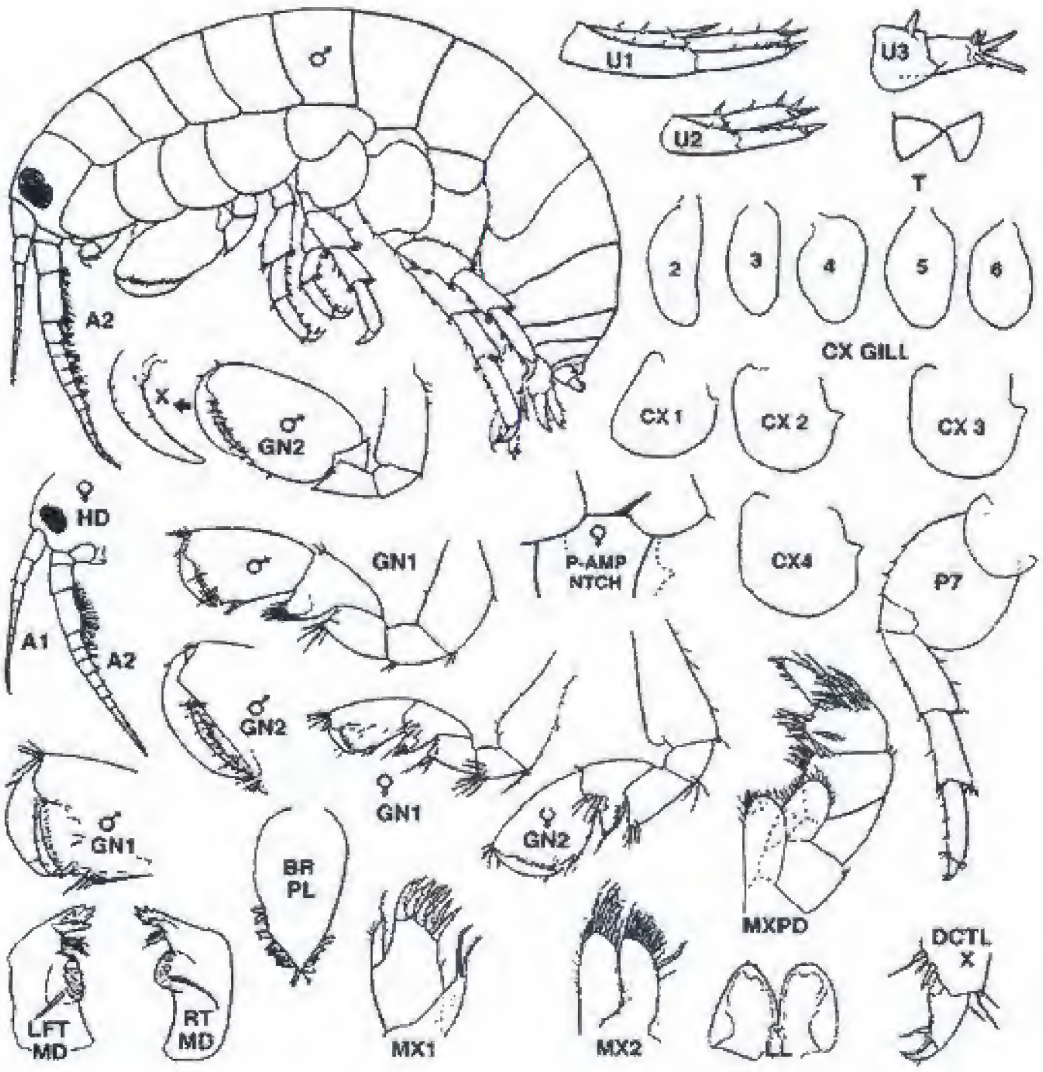

Fig. 51. *Ptilohyale barbicornis* Hiwatari & Kajihara, 1981b. Male (11.6 mm); female ov (9.2 mm). Shore near Tokyo, Japan (modified from Hiwatari Kajihara1981b+ CMN collections).

ata (Hiwatari & Kajihara, 1981a); *A. stebbingi* (Chevreux, 1888); *?Apohyale tristanenis* (Macnae, 1953); **A. uragensis* (Hirayama, 1980); *A. wakabarae* (Serejo, 1999); *Apohyale sp. (=Hyale media* of Hurley 1957).

Diagnosis: Body medium to large, robust, smooth,often strikingly pigmented. Eyes medium large, usually broadly reniform, nearly meeting mid-dorsally. Antennae short. Antenna 2, peduncular segments 4 & 5 stout, nearly bare; flagellum short (<20 segments), weakly (or not) setose posteriorly

Mandible, left lacinia 5- 6-dentate. Maxilla 1, palp 1-segmented, short to medium, not extending beyond base of apical spines of outer plate. Maxilla 2, plates slender, inner plate with single inner marginal seta. Maxilliped palp stout, segment 2 broader than long, dactyl normal, not sexually dimorphic (lacking apical whip seta in male).

Coxa 1 broadened distally, smooth; coxae 1-4 with distinct hind marginal cusp in both sexes. Coxa 5 mostly antero- to aequilobate. Coxae 6 and 7 posterolobate. Coxal gills plate-like, largest posteriorly.

Gnathopod 1 normal, slightly sexually dimorphic; bases, hydrodynamic lobe weak or lacking; carpal lobe distinct, broad; propod slightly broadening distally, lacking mediofacial guiding spine (♂); dactyl simple. Gnathopod 2 strongly sexually dimorphic; basis (male) with weak to medium hydrodynamic lobe; carpus short, posterior lobe usually lacking (often very thin, short); propod large, variable.

Peraeopods 3-7 stout, dactyls short, with distinct inner marginal seta. Peraeopods 5-7, bases broad, margin nearly smooth, notch and surge seta variously developed; segment 4 relatively short and broad; segment 6, inner distal locking spine variously developed, rarely striated.

Epimeral plates 2-3 smooth below, hind corners acuminate. Pleopods normal. Uropod 1, peduncular distomedial and lateral spines typically short, weak; rami with marginal and strong apical spines. Uropod 2, outer ramus the shorter, with few marginal spines. Uropod 3 uniramous; ramus short, blunt, not longer than peduncle, with apical, and occasionally posterodorsal, marginal spine(s).

Telson lobes subtriangular, usually short, apical margins unarmed.

Female: Gnathopod 1, hydrodynamic lobes lacking; propod deep. Gnathopod 2 always larger, often strong; basis with weak hydrodynamic lobe. Brood plate (Gn2) very large, proximally broad, narrowing distally to acute apex; marginal setae very short, numerous. Preamplexing notch simple, shallow, obtuse; unguisial groove lacking or very short; peraeon 2, posteroventral lobe medium to large.

Etymology: From the Greek root "*apo*" meaning "advanced", and the Greek root name "*Hyale*", in reference to the advanced nature of several character states of component species.

Distributional Ecology: This genus is widespread around boreal and temperate rocky coastlines of North and South Pacific oceans, less frequent in the tropics. Species are strictly intertidal, mainly on rocky shores, ranging often into brackish (occasionally hypersaline) spray pools of the supralittoral zone. All are saltators in air, some (e.g., *A. pugettensis)* apparently as capably as some members of the Talitridae.

Remarks: The largest and most advanced species occur highest in the tidal zone, and tolerate wide extremes of temperature and salinity . Thus, *Apohyale prevosti* (M-E.) *(= H. nilssoni)* lives well up into winter-iced regions of the North Atlantic such as Iceland, Labrador, and the upper St. lawrence estuary.

Apohyale pugettensis and *A. californica* share advanced character states with western Pacific counterpart species *A. bassargini* and *A punctata*, and to lesser extent with the central Pacific (Hawaiian) *A. bishopae*. By contrast, the less terrestrial *A. anceps* evinces relatively plesiomorphic character states. Members of genus *Apohyale* (e.g. *A. crassipes*) have high diploid chromosome numbers (~50) and high karyotype formula (19); in the same range as *Parhyale* (48 and 24 resp.) (see Libertini and Krapp-Schickel 2001)

The old generic name, *Nicea* Nicolet, 1849, originally applied to a Peruvian intertidal species (probably a member of the *grandicornis* group and part of genus *Apohyale*) is now invalid because of ICZN 50-year non-usage rule).

The commensal relationships of *Hyale grandicornis* (fide J. L. Barnard) to acmaeid limpets, occurring in lower to upper tidal levels along rocky shores of central California, has been studied by Johnson (1968). The mottled immature hyalid amphipods (1-6 mm in length) apparently actively seek the moist protection of the nuchal cavity and pallial groove of the underside of larger shells (> 8 mm in length) of 5 species of *Acmaea* and *Lottia gigantea*. The hyalids apparently feed on algae growing on the surface of the limpet shells.

The identity of this hyalid species remains moot. Adult animals were never found with the young hyalids. *Apohyale californica* (J. L. Barnard, 1969b) is a common hyalid species at MW-LW levels in the Monterey Bay region. However, the senior author (ELB) has also collected adult specimens of *A. pugettensis* in HW pools of the Monterey peninsula (p. 112). The external body pattern of females and immatures of *A. pugettensis* is often mottled, whereas adult males are often marked by a large mid-dorsal whitish area, giving the larger animals a "saddle-back" appearance. Since adults of *A. pugettensis* are frequent inhabitants of HW spray pools where conditions of temperature, salinity, and desiccation may become extreme and unsuitable for growth, immature animals may therefore frequent less rigorous intertidal niches. Presumably these occur at somewhat lower intertidal levels, in this instance provided by ever-present living specimens of *Acmaea*. Further study of the complete life cycle of this commensal hyalid amphipod species is indicated.

Apohyale anceps (J. L. Barnard)
(Figs. 52, 53)

Allochestes anceps Barnard, 1969b: 130, figs 25, 26.
Hyale anceps Barnard 1974: 42;—Barnard 1979: 114;—Barnard & Karaman 1991: 369.
Apohyale anceps Bousfield 1981: 80;—Bousfield 2001a: 104.

KEY TO NORTH PACIFIC AND SELECTED WORLD SPECIES OF *APOHYALE*

(* North Pacific Species)

1. Antenna 2, basal flagellar segments setose; uropod 3, peduncle with 2 posterodistal spines; peraeopods 5-7, dactyls with small inner marginal setae ..... 2.
Antenna 2, basal flagellar segments essentially bare; uropod 3, peduncle with single posterodistal spine; peraeopods 5-7, dactyls with medium stout inner marginal seta ..... 4.

2. Uropods 1 & 2, outer ramus lacking marginal spines; uropod 1, peduncular distolateral spine large (> 1/3 outer ramus); Hawaii ..... *A. *ayeli* (Barnard)
Uropods 1 & 2, outer ramus with 1-2 marginal spines; uropod 1, peduncular spine short ..... 3.

3. Gnathopod 2 (mature♂) carpal lobe present; peraeopods 5-7, locking spine of segment 6 small, simple; mandibular left lacinia 5-dentate ..... *A. *anceps* (Barnard) (p. 106)
Gnathopod 2 (♂), carpal lobe lacking; peraeopods 5-7, locking spine large, striated mandibular left lacinia 6-dentate; N.Z. ..... A. *media* (Dana)

4. Gnathopod 2 (♂), basis with large rounded anterodistal lobe, partly masking ischium; uropods 1 & 2, outer ramus with 0-1 marginal spines; N. Atlantic. ..... *A. prevostii* (M.-E)
Gnathopod 2 (♂), basis with small anterodistal lobe not masking ischium; uropods 1 & 2, outer ramus with 2-4 marginal spines. ..... 5.

5. Gnathopod 2 (♀), propod distinctly larger and of differing form than in gnathopod 1; large species ..... 6.
Gnathopods 1 & 2 (♀), propods differing little in size and form; small species ..... 8.

6. Uropod 2, outer ramus with 3-4 marginal spines; uropod 3, ramus slender longer than peduncle, with 2 marginal spines ..... *A. grandicornis novaezealandiae* Thomson
Uropod 2, outer ramus with 2 marginal spines; uropod 3, ramus short, thick with 0-1 marginal spines ..... 7.

7. Eyes large; uropod 3, ramus with 1 marginal spine ..... *A. pugettensis* (Dana)(p. 110)
Eyes small; uropod 3, ramus lacking marginal spines ..... *A. bassargini* (Derzhavin) (p. 112)

8. Antenna 2, flagellum medium long (15-segmented); uropods 1 & 2, outer ramus with 4 spines; mandibular left lacinia 6-dentate (Japan) ..... *A. *uragensis* (Hirayama)
Antenna 2, flagellum short (10-14 segmented); uropods 1 & 2, outer ramus with 1-3 marginal spines; mandibular left lacinia 5-dentate ..... 9.

9. Peraeopod 6, basis uniformly rounded behind as in peraeopods 5 & 7 ..... 10.
Peraeopod 6, basis relatively narrow, not rounded behind as in peraeopods 5 & 7 .....
..... *A. californica* (Barnard)(p. 113)

10. Antenna 2, flagellum 14-segmented; epimeral plate 2, hind corner produced ..... 11.
Antenna 2, flagellum 10-13 segmented; epimeral plate 2, hind corner acute, not produced ..... 12.

11. Uropod 3 ramus > peduncle; gnathopod 2 (♂) palm strongly oblique, elongate, length > 2X posterior margin of propod ..... *A. humboldti* (Barnard)
Uropod 3, ramus < peduncle; gnathopod 2 (♂), palm regularly oblique, length ~1.5 X posterior margin ....
..... *A. wakabari* (Serejo)

12. Antenna 2, flagellum 10-segmented; uropod 2, outer ramus about equal in length to inner ramus; uropod 3, ramus with 1 marginal spine ..... *A. *bishopae* (Barnard)
Antenna 2, flagellum 12-13-segmented; uropod 2, outer ramus distinctly shorter than inner; uropod 3, ramus lacking marginal spine ..... *A. punctata* (Hiwatari & Kajihara) (p. 114)

Material Examined:

ALASKA

Aleutian Islands: Banjo Pt, Amchitka I., C. E. O'Clair Stn B-2, 1973 - 1 ♂ (13 mm)(slide mount), 1 ♀ ov (11 mm) (slide mount) (**fig'd**); Ibid, Stn. IA-2, 1972 - 1 ♂.

Southeastern Alaska: ELB Stn, 1980: S18B2 (1 ♀).

BRITISH COLUMBIA

North Central coast: ELB Stn H65, Christie Pass, July, 1964 - 1 ♂.

Southern Vancouver I.: ELB Stn. P4, July 5, 1955 - 1 ♂ (9.5 mm)(slide mount) (**fig'd**), CMNC2002-0095; 1 ♀ ov (8.5 mm)(slide mount)(**fig'd**); + 3 ♀♀ ov (to 7 mm).

C. Lobban Stns, 1971: CL 1004 (Rocky Pt.,Wickaninnish Bay - 4 ♂♂, 7 ♀♀, 13 im; CL 1006 - 27 im; CL1028 - 1 ♂, 6♀♀, 2 im.; CL 1032 - 2 ♀♀, 4 imm.

WASH.-ORE

Sunset Bay, Oregon, K. E. Conlan Stn 06-5, 1986 - 7 ♀♀.

CALIFORNIA

Monterey Bay, in *Entocladia*, LW, P. Glynn coll., 1959 - 6 lots containing 9 ♂♂, 80 ♀♀, 47 im. CMN Acc. No. 61-37.

Diagnosis: Male (9.5 mm): Eyes medium subovate, dorsolaterally positioned. Antenna 1, peduncular segment 2 & 3 short; flagellum 8-10 segmented. Antenna 2 short, pedunclear segments 4 & 5 with posterodistal tufts of setae; flagellum short, 10-12 segmented, segments with postero- and anterodistal setal tufts,

Buccal mass slightly prognathous. Mandible, left lacinia 5-dentate, spine row with 2-3 accessory blades. Maxilla 1, palp slender, extending beyond base of apical spines of outer plate. Maxilliped palp segments short, stout; dactyl conical, nail small.

Coxa 1-3 slightly broader than deep, lower margins rounded, each with posterior shelf and weak cusp. Coxa 4 broader than deep, with small posterior cusp and small proximoposterior excavation. Coxa 5 shallowly anterolobate, anterior lobe larger than posterior lobe. Coxa 6 posterolobate. Coxa 7 deep, broadly rounded below. Coxal gills narrowly sac-like.

Gnathopod 2, hydrodynamic lobes on basis and ischium very small; carpus stout, lobe relatively broad and deep, lower margin with 6-8 short comb setae; propod medium, broadening distally, palmar margin gently convex, unevenly spinose, shorter than posterior margin having small distal setal cluster; dactyl stout, slightly overlapping palm. Gnathopod 2 large; hydrodynamic lobe on basis medium, rounded, lacking on ischium; merus posterodistallly acute; carpal lobe thin, extending below merus, lower margin with a few comb setae; propod smoothly and deeply subovate, palm oblique, slightly convex, shorter than smooth posterior margin; dactyl regular, fitting palm.

Peraeopods 3 & 4 medium, segment 5 strong, segment 4 shorter than 5 & 6, clasping spine small; dactyls short. Peraeopods 5-7, bases broad, regularly rounded behind, hind margins each with notch and surge seta; segment 5 shorter than segments 4 & 6, anterior margin of segment 6 with 3-4 weak spines; dactyls medium short, inner margin distally with medium seta and minute castellations.

Epimeral plate 1, hind corner obtusely rounded, plates 2 & 3, hind corners squared, hind margin with minute setae. Pleopods regular. Uropod 1, peduncle, outer margin with 3-4 spines of unequal length; outer ramus slightly shorter than inner ramus, with 2 short marginal and a few longer apical spines. Uropod 2, rami subequal, inner ramus with 1-2 short marginal spines. Uropod 3 short, peduncle with 2 unequal posterodistal spines; ramus stout, slightly shorter than peduncle, with 3-5 unequal apical spines.

Telson lobes short, apices bluntly rounded, weakly setulose.

Female ov (8.5 mm): Gnathopod 1, basis with weak hydrodynamic lobe; lacking in ischium; carpal lobe small; propod subrectangular, not broadening distally, palm short, oblique. Gnathopod 2 similar to gnathopod 1 but basal hydrodynamic lobe more prominent, carpal lobe larger, and propod distinctly larger, with gently convex lower margin. Brood lamella 2 broadly heart-shaped, narrowing to subacute apex; margins with numerous (>150) medium short, hook-tipped brood setae. Preamplexing notch squared or slightly obtuse; unguisial groove elongate, shallowly oblique; posterodistal lobe of peraeon segment 2 shallow, extending far forward, anterior margin nearly vertical.

Distributional Ecology: Among algae on rocky shores, LW to immediate subtidal, Aleutian Islands and southeastern Alaska to Oregon, sporadically south to central California.

Remarks:

Apohyale anceps is a relatively primitive and more aquatic member of the genus, not closely related to *A californica* and *A. pugettensis* with which it overlaps throughout its range. Its affinities are closer to *A. ayeli* (Hawaii) and a few other species with weakly developed carpal lobe of gnathopod 2 (male).

A. anceps exhibits some character states that are more typical of genus *Ptilohyale*. These include the

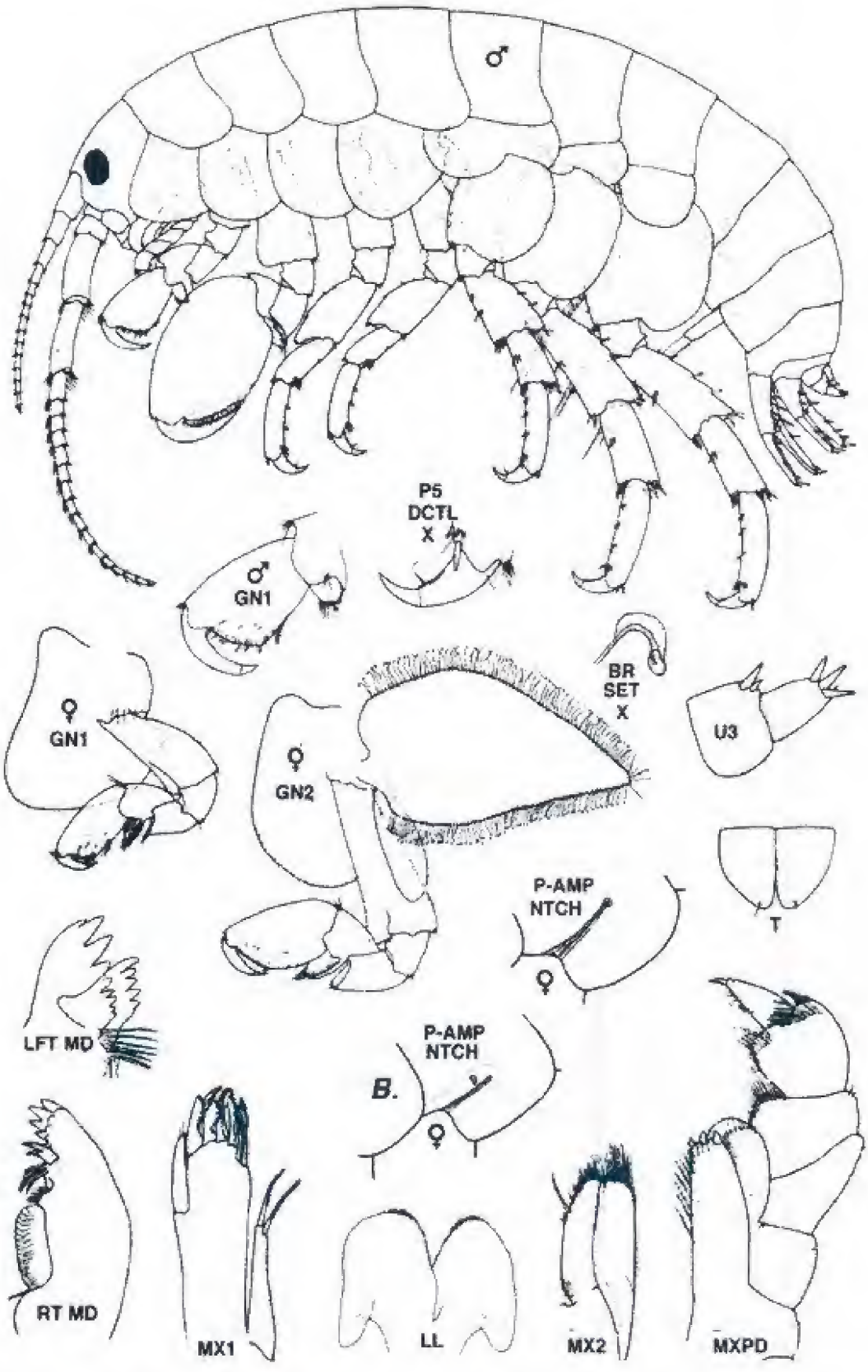

Fig. 52. *Apohyale anceps* (Barnard, 1969). Male (9.5 mm); female ov (8.5 mm). ELB Stn P4 , NW end Wickaninnish Bay, Vancouver I, B. C.
B. Female ov (11 mm). Amchitka I., Aleutian Islands.

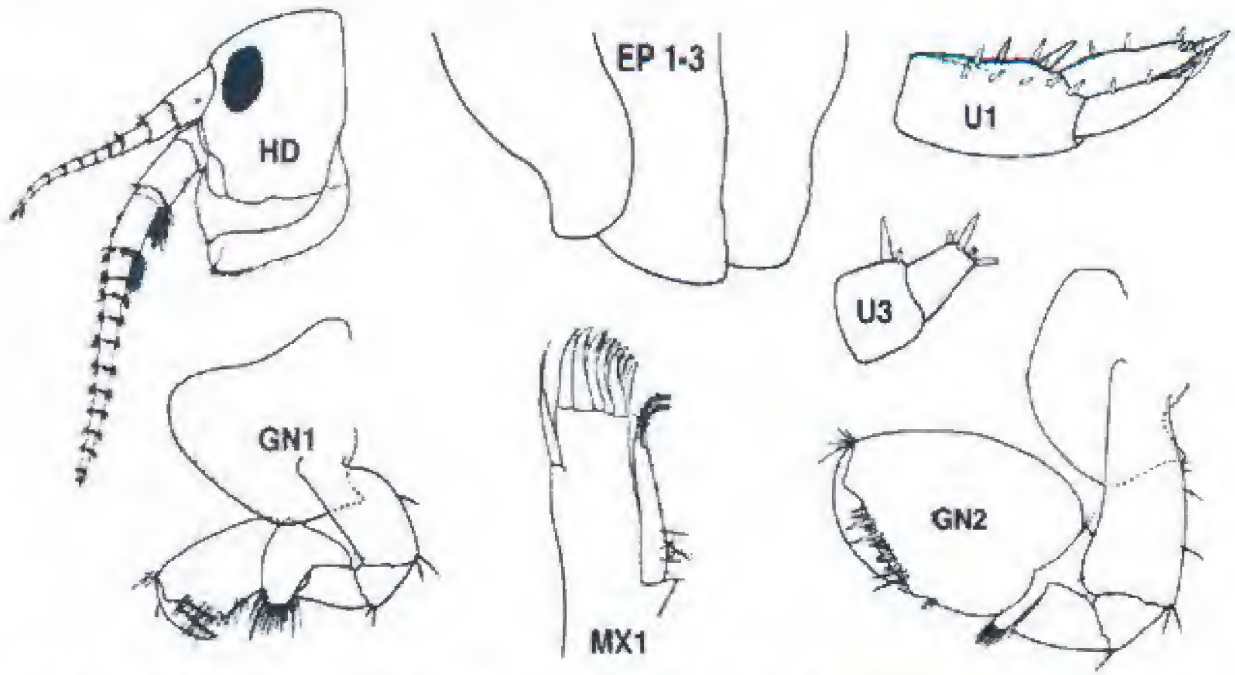

Fig 53. *Apohyale anceps* (Barnard, 1969b) Male (8.0 mm). Hazard Canyon Reef California. (modified from Barnard 1969b).

moderately setose basal flagellar segments and peduncular segment 5 of antenna 2 (male); the slightly elongate distomedial spine of the peduncle of uropod 1 and, in the female, the more strongly impressed unguisial groove of the preamplexing notch (Figs. 14 & 52).

The species exhibits a north-south geographical cline in some character states. Populations in the Aleutians tend to be larger than those in central and southern regions (males 13 mm vs 8 mm), the antennae are more strongly setose, and the inner margins of the peraeopod dactyls tend to be more strongly pectinate. However, most character states, including the preamplexing notches of females, are virtually identical (Fig. 53).

Apohyale pugettensis (Dana)

(Fig. 54)

Allorchestes pugettensis Dana, 1853: 901, t. 61, figs. 6a-d.
Hyale pugettensis Bulycheva 1957: 111;—Bousfield 1981: 79, figs. 9,10;—Austin 1985: 595;—Staude 1987: 379;—Barnard & Karaman, 1991: 370.
Apohyale pugettensis Bousfield 2001a: 104.
non: *Hyale* sp. (Ricketts & Calvin 1948: #153)

Material Examined:
~750 specimens in 85 lots, Aleutians to Oregon and central California. ELB Station references: Bousfield (1958, 1963, 1968), Bousfield & McAllister (1962); Bousfield & Jarrett (1981).

ALASKA
Aleutian Islands: Amchitka I., C. E. O'Clair Stn. IA-2, 1971-74, 17 collns. - 46 specimens; Stn IA-3, 1972-73, 2 collns. - 5 specimens. Unimak I., C. E. O'Clair Stn. IA-2, 1973 1 im specimen.
Southeastern Alaska: ELB Stns, 1961: A5(1), A 19 ((1), A22 (1), A23 (5), A57 (7), A162 (13).
ELB Stns 1980: S7B2 (9♂♂, 6 ♀♀).

BRITISH COLUMBIA
Queen Charlotte Islands: ELB Stns, 1957: E14a E21(7+2); H14 (44), H15 (15); W6 (18), W16 (1).
North Central Coast ELB Stns, 1964: H24, Cox Pt.,Trutch I. (53°08'N ,129°45'W), HW level - 1 ♂ (18.0 mm) **Neotype** (slide mnt.), CMNC 1983-1534, H48 (2). H53 (1), H57 (1).
South Central Coast: ELB Stn M2 (Emmond's Beach) - 4 ♂♂, 11 ♀♀.
Northern Vancouver Island: ELB Stns, 1959: N1 (17); O1 (5), O2 (4), O5 (11), O11 (1), O15 (4), O17 (21); V4a (20), V19 (4).
Southern Vancouver Island: ELB Stns, 1955: F5 (8); P4 (7), P5, NW end of Long Beach, Wickaninnish Bay, rock pools at and above HW level, Aug. 2 - 1m. (18 mm) (slide mount)(**fig'd**): 1 ♀ ov (12 mm) (slide mount) (**fig'd**). C + 35 ♂♂, ♀♀; P6 (7).
ELB Stn, 1964: H44 (12)
ELB Stns, 1970: P701 (5), P702 (14), P704 (21), P708 (13), P711 (1), P712 (2), P714 (150), P719 (5).
ELB Stns, 1975: P3b (1), P5e (5), P16a (7).
ELB Stns. 1976: B28 (6), N10 (11).

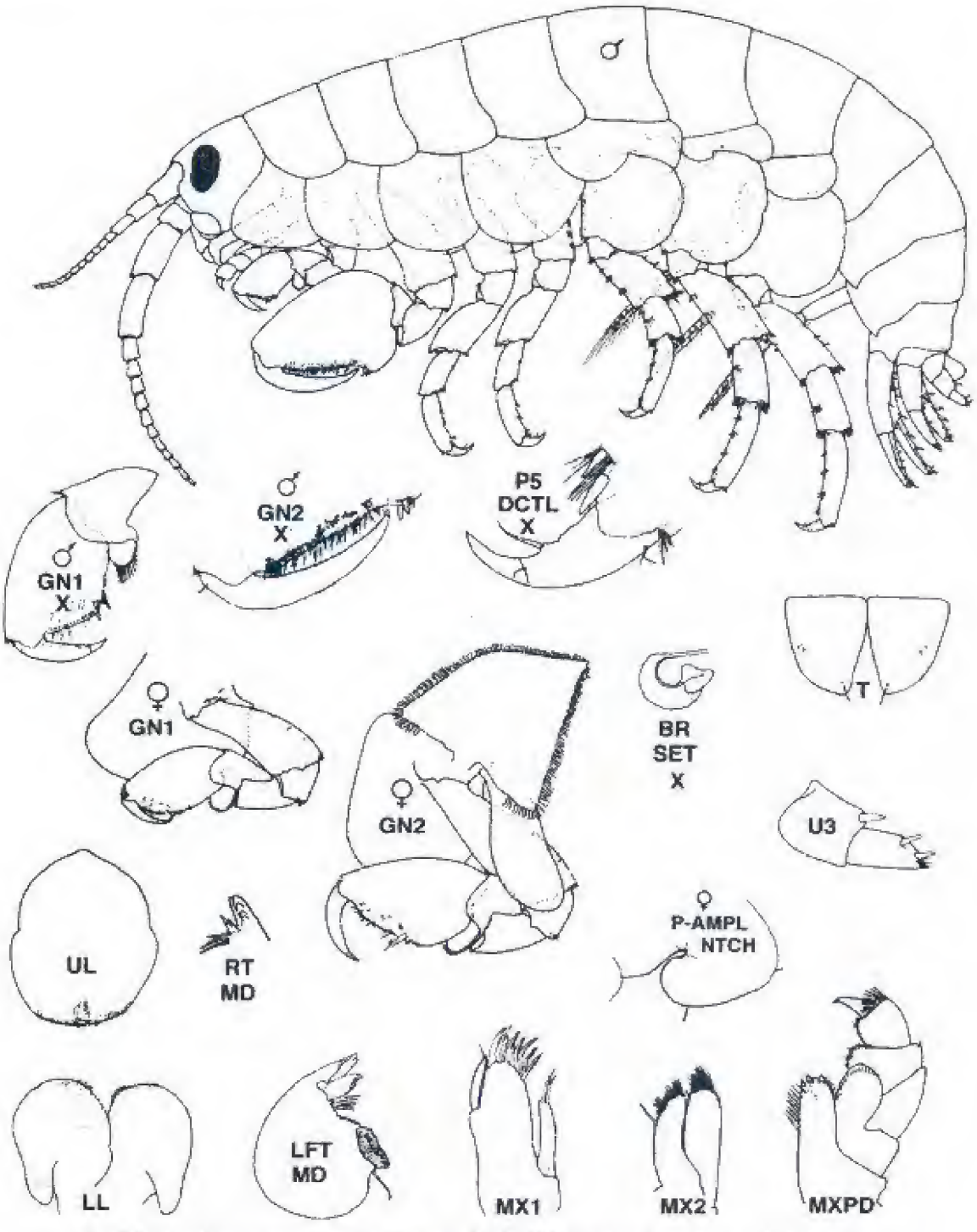

Fig. 54. *Apohyale pugettensis* (Dana). Male (18.0 mm); female ov (12.0 mm). NW end Long Beach, Vancouver I., B. C.

ELB Stns. 1977: B6b (6), B10 (1), B11 (1), B12 (10).

WASH-OREGON

ELB Stns. July-Aug., 1966: W22 (2 fem), W29 (6), W35 (22), W36 (16) W40 (4), W45 (1). W52 (5), W57 (22), W58 (1 im).

CALIFORNIA

Monterey Bay, HW pools, ELB coll., July, 1959 - 2♂♂, 1♀.

Additional Material

British Columbia: Long Beach, V. I., M. L. Florian coll., 1963 - 3♀♀, 9 im; Rock I. Wouwer I., C. Lobban coll, 1973: sev. spms; Victoria, HW pools, R. Long coll., May, 1977 - ♂ (13 mm) (slide mount), ♀ (7 mm) (slide mount); Port Alice, C. Cross coll., 1979 - 1 spm; Wouwer I., C. Levings coll. - several spms; Gregory I., G. C. Carl coll., 1958 - several ♂♂, ♀♀.

Northwestern USA. T. Suchanek coll., 1976-77: Tatoosh I.

(5), Olympic peninsula (10), San Juan I. (18), all ; San Juan I., C. Staude coll., 19??- 1 subad. ♂ (9.5 mm)(slide mount); San Juan I., R. M.O'Clair, Aug./76 - subad. ♀(5.8 mm) (slide mount).

Diagnosis: Male (to 18 mm). Body large, brightly pigmented in "saddle-back" pattern. Eyes medium large, lenticular, dorsolaterally positioned. Antenna 1, peduncular segments 2 & 3 not shortened; flagellum 10-12 segmented. Antenna 2 short (< 2X antenna 1), peduncular segments 4 & 5 stout, smooth, subequal; flagellum smooth, 10-12 segmented.

Upper and lower lips regular, apically weakly pilose. Mandible, left lacinia 5-dentate, spine row with 4 accessory blades; right lacinia bifid, with 3 blades. Maxilla 1, palp slender, medium, tip slightly exceeding base of spine teeth of outer plate. Maxilla 2, distal setae of plates retricted to apical region. Maxilliped, palp segment 3 very short broad; unguis subconical, curved, shorter than palp segment 3, unguis small.

Coxae 1-3 as broad as deep, lower margins broadly rounded, hind marginal cusps prominent. Coxa 4 not broader than deep, rounded below, posterior excavation normal. Coxa 5 shallowly anterolobate. Coxa 6 shallowly posterolobate. Coxa 7 broader than deep. Coxal gills narrowly sac-like.

Gnathopod 1 basis and ischium virtually lacking hydrodynamic lobes; carpal lobe short, posterior lobe medium, lower margin with ~15 short comb setae; propod deep, slightly broadening distally, Gnathopod 2, propod short, deep, palmar margin gently convex, unevenly spinose, much longer than smooth convex posterior margin.

Peraeopods 3 & 4, distal segments weakly spinose, clasping spine vestigial. Peraeopods 5-6, bases broad, regularly rounded behind; segment 4 broadened, short, segment 5 short.

Uropod 1, peduncle with 2-3 short outer marginal spines; outer ramus with 2 short marginal spines. Uropod 2, outer ramus with 1-2 short marginal spines. Uropod 3 peduncle with 1 posterodistal spine; ramus tapering, slightly shorter, with 1 posterodistal marginal and 2-3 apical spines.

Telson lobes short, apices bluntly rounded.

Female ov (12.0 mm): Gnathopods markedly dissimilar in form and size. Carpal lobe of gnathopod 2 slender, deep. Brood lamella 2 short, very broad narrowing to acute apex; marginal setae very short. Preamplexing notch sharply incised; unguisial groove short, arched; posterodistal lobe of peraeon 2 relatively shallow, broad, smoothly rounded anteriorly.

Distributional ecology: Frequently occurring in spray pools often nearly fresh to the taste,at and above HW level along bedrock shores, from southern Alaska to central California.

Remarks: Character states of the present extensive material closely match those of the original illustrations of Dana (1853, figs. 6a-d), including the left mandible. The species is closely related to *A. californica, A. bishopae* of the Hawaiian islands and *A. punctata* and *A. bassargini* of Japanese and Russian shores.

The type material of Dana (1853) appears no longer available. Accordingly, neotype specimens from the coast of British Columbia are designated above.

Apohyale bassargini (Derzhavin, 1937)

Hyale bassargini Derzhavin, 1937: 93, pl. 4.2;—Gurjanova 1951: 817, fig. 572.
Hyale novaezealandiae Bulycheva 1957: 100, fig. 36.

Remarks: Dr. Takeheko Hiwatari (pers. comm.) is in the process of redescribing this large intertidal counterpart species of *A. pugettensis* that ranges along both coasts of the Sea of Japan to the west coast ofthe south Sakhalin I., Russia (Bulcheva 1957). Regrettably, diagnostic features of the gnathopods, brood plates, and preamplexing notch have not yet been described, These, as well as saltation ability, may be similar to those of *Apohyale pugettensis*.

Apohyale bassargini differs from *A. pugettensis* by character states of the key, and the following features: (1) in pereopods 3-7, the paired locking spines are similar in size (vs. distalmost spine slightly the larger); (2) in uropod 3, the ramus is short and broad, and subequal to the peduncle (vs. ramus slender and slightly longer than peduncle), (3) in the telson, the lateral margin of each lobe has 4 small plumose setules (vs. tip of each lobe has a single seta).

Apohyale californica (Barnard)
(Fig. 55)

Hyale grandicornis californica Barnard, 1969b: 133, figs. 27-28.
Hyale californica Barnard 1979: 116;—Bousfield 1981: 84, fig. 10;—Barnard & Karaman 1991: 369.
Apohyale californica Bousfield 2001: 104.

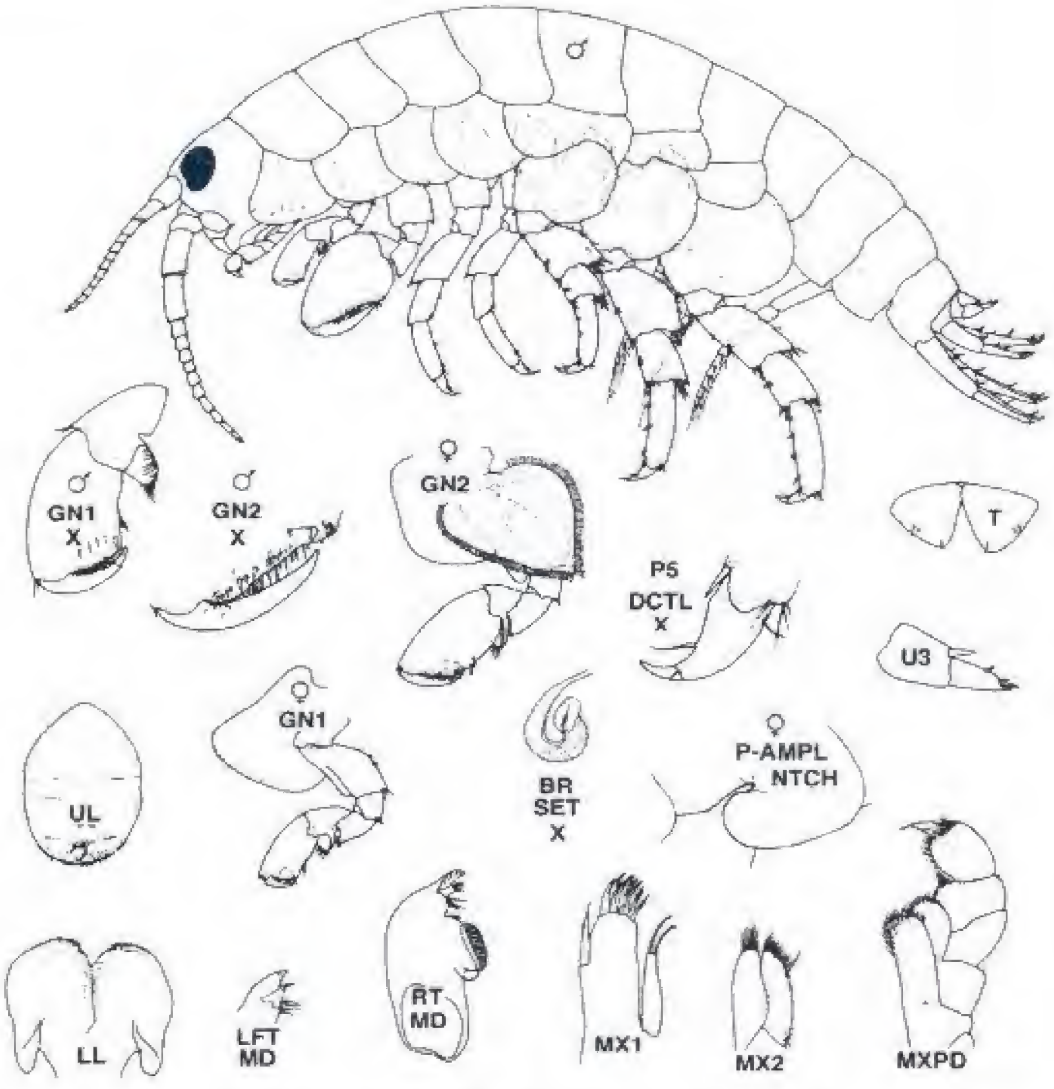

Fig. 55. *Apohyale californica* (Barnard, 1969b). Male (8.0 mm); female ov (6.0 mm). Monterey Bay. CA

Material examined:

BRITISH COLUMBIA

South Central coast: ELB Stns 1955: M2, Emmond's Beach - 4 ♂♂, 11 ♀♀.

Northern Vancouver I.: ELB Stns, 1959: O11, Hesquiat at Matlakaw Pt. - 1 ♀.

Southern Vancouver I.: Long Beach, M. L. Florian coll., 1963- 3 ♀♀, 9 imm.

WASH.-OREGON

ELB Stns, 1966: W22, Pt. Grenville, south side Gray's Hbr., WA - 2 ♀♀; W36 Clallam Bay, WA - 3 ♀♀, 12 im; W58, Seal Rocks, ORE. - 1 im.

CALIFORNIA

Monterey Bay, P. Glynn coll., May 25/59 - 1♂ (8.0 mm) (slide mount)(**fig'd**), CMNC 2002-0094; 1 ♀ (6.0 mm) (slide mount)(**fig'd**), NMCC 1961-37; Ibid, in *Endo-cladia*, 1960 - 1♂, 3♀♀.

San Diego, W. L. Klawe coll, 1956 - 5 ♂♂, 7 ♀♀.

MEXICO

Turtle Bay, W. L. Klawe coll., 1958 (2 lots) - 2 ♂♂, 6 im., NMCC Acc. No. 6174.

Diagnosis: Male (8.0 mm): Eyes large, broadly almond-shaped, nearly meeting mid-dorsally. Antenna 1, peduncular segment 2 distinctly longer than 3, flagellum 9-10 segmented. Antenna 2 short (<2X antenna 1), peduncular segments 4 & 5 subequal in length; flagellum smooth, 10- 12-segmented.

Mandible, left lacinia 5-dentate, spine row with 4 accessory blades; right mandible with 3 blades. Maxilla 1, palp short, tip barely reaching base of spine teeth of outer plate. Maxilliped, palp segments stout; dactyl curved. shorter than palp segment 3.

Coxae 1-3 slightly broader than deep, lower margins gently convex, hind margins with prominent cusp. Coxa 4 broader than deep, posterior excavation

regular. Coxa 5 anterolobate, anterior lobe larger than posterior lobe. Coxa 6 shallowly posterolobate. Coxal gills sac-like, large on peraeopod 6.

Gnathopod 1, hydrodynamic lobe of basis weak, lacking on ischium; carpal lobe medium broad, margin with about 15 comb setae; propod subrectangular, slightly arched, palm nearly vertical, lower margin with distal group of short setae; dactyl regular. Gnathopod 2, hydrodynamic lobe small; carpal lobe minute; propod large, subovate, narrowing distally, palm oblique, with slight hinge tooth, slightly longer than smooth convex posterior margin; dactyl, tip barely reaching paired palmar spines.

Peraeopods 3 & 4 stout, segment 6 posterior marginal spines few, weak; dactyls short. Peraeopods 5-7 stout; bases broadly expanded, rounded posterior margins weakly crenulate, each with small notch and surge seta. Peraeopod 5, segment 4 broad, segment 5 short, with strong posterodistal clusters of short spines. Peraeopods 6 & 7, segment 6 slightly longest, with weak anterior marginal spines; dactyls short.

Epimeral plates 2-& 3, hind corners finely acuminate. Pleopods regular. Uropod 1, peduncle with 2-3 short outer marginal spines; rami with 1-2 short marginal spines. Uropod 2, rami with 2 short marginal spines. Uropod 3 peduncle with single posterodistal spine; ramus tapering, slightly shorter, with 1 posterodistal marginal and 2-3 apical spines.

Telson lobes short, broad apices bluntly rounded.

Female ov (6.5 mm) Gnathopod 1 virtually lacking basal and ischial hydrodynamic lobes; propod suBrectangular, similar to that of male. Gnathopod 2, basis with medium lobe; carpus short, posterior lobe relatively long and narrow; propod similar to, but heavier than in gnathopod 1. Brood lamella on peraeopod 2 broadly heart-shaped, narrowly to broadly acute apex. Preamplexing notch sharply incised; unguisial groove short, curved; posterodistal lobe of pearon segment 2 large, smoothly rounded anteriorly.

Distributional Ecology: Washington to Pt. Conception, California, south to La Jolla, and northern Mexico (Barnard 1979), algal turf, MW-LW level.

Remarks: As noted in the key to species (p. 107) *Apohyale californica* is less closely related to *A. anceps* than to *A. pugettensis* with which it overlaps distributionally and ecologically in the northern part of its range.

Apohyale punctata (Hiwatari & Kajihara)
(Fig. 56)

Hyale punctata Hiwatari & Kajihara, 1981a: 26, figs. 4-6;—Barnard & Karaman 1991: 370 ;—Ishimaru 1994: 68.

Remarks: Selected characters of *Apohyale punctata* illustrate character state of coxal plates, coxal gills, and sexual dimorphism typical of genus Apohyale, but not as clearly shown in illustrations of North American species.

A. punctata is allied with *A. uragensis* Hirayama, *A. californica* Barnard, and other warm-temperate and tropical species of the genus. Their character states include relatively small size, and propods of the female gnathopods 1 & 2 that differ little in size (see key, p.107). *Apohyale anceps* exhibits the primitive character states that overlap to some degree with those of genus *Ptilohyale*. These include a partially setose flagellum of antenna 2, a per-sistent carpal lobe in gnathopod 2 of the adult male, a preamplexing notch with distinct unguisial groove, and a low intertidal, semi-aquatic life style.

***Serejohyale* n. g.**

Hyale spinidactyla complex Serejo, 2001: 479, Table 1, fig. 8, and key.

Type species: *Hyale spinidactyla* Chevreux, 1926 (present designation)

Species: *Serejohyale spinidactyla* (Chevreux, 1926: 366, figs 13,14);—Reid, 1951: 245, fig. 39);—Arresti 1996: 79, figs. 2-8;—Serejo 2001: 480, figs. 1-2; *S. ramalhoi* (Reid, 1939: 29 , figs. 1-2);*S. spindactyloides* (Schellenberg, 1939: 130, figs. 17-22); *S. youngi* (Serejo, 2001: 484, figs. 3-7).

Diagnosis: Body smooth, medium in size. Antennae medium, unequal. Antenna 1, peduncular segments not shortened. Antenna 2, peduncle 4 and flagellar segments not (or little) plumose-setose posteriorly. Eyes large, subrectangular to subovate.

Mandible, left lacinia 6-9 dentate; blades of spine row 2-4(5). Maxilla 1, palp 1-segmented, short. Maxilla 2, plates slender, inner plate with 2 unequal proximal inner marginal plumose seta. Maxilliped palp, base of outer plate large; dactyl short, unguis short.

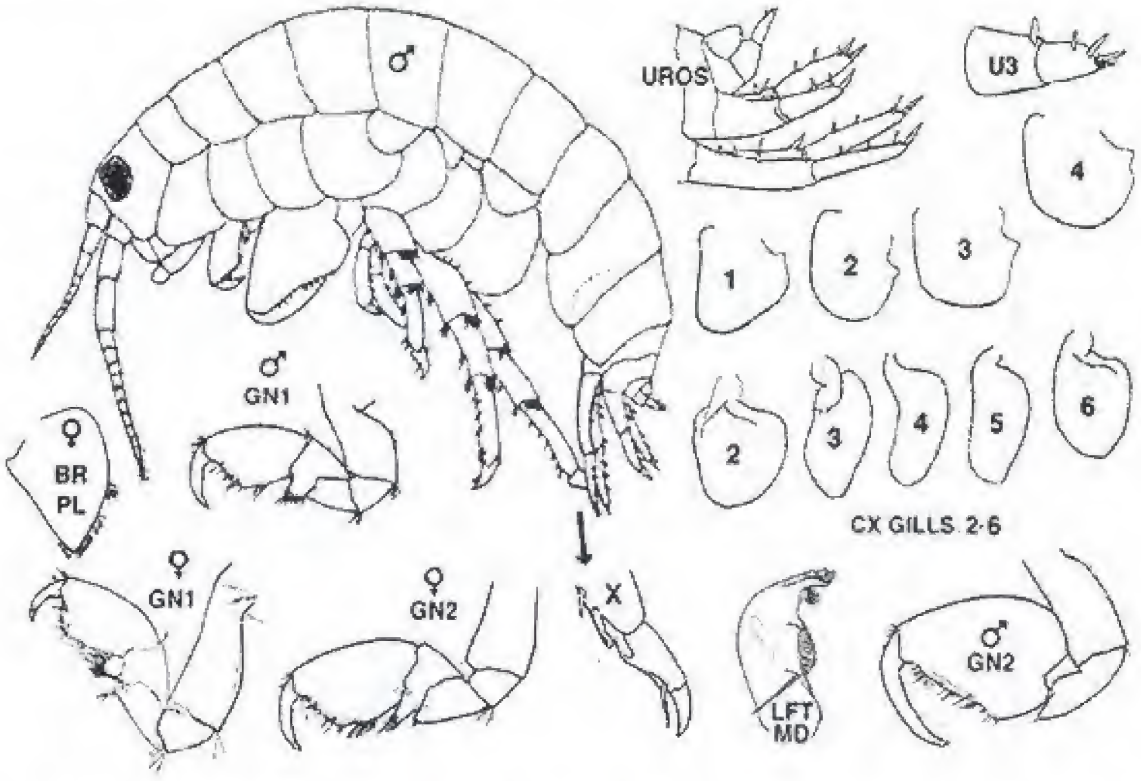

Fig. 56. *Apohyale punctata* (Hiwateri & Kajihara, 1981). Male (12.0 mm); female ov (8.5 mm). Kyushu, Japan; intertidal. (after Hiwatari & Kajihara 1981a).

Coxae 1-4 shallow, broader than deep, with posterior marginal cusp. Coxae 5 markedly anterolobate. Coxae 6 & 7 posterolobate. Coxal gills appearing short, sac-like.

Gnathopod 1 normal, slightly sexually dimorphic; basis, anterodistal lobe medium; carpal lobe distinct broad; propod slightly broadening distally, lacking medial facial guiding spine (male); dactyl simple. Gnathopod 2 strongly sexually dimorphic; basis (male) with medium to strong anterodistal lobe; ischium lobate; carpus lacking posterior lobe; propod subovate, palm elongate, strongly oblique, with weak hinge tooth, dactyl elongate, with hinge tooth.

Peraeopods 3-7, dactyls inner margin striate, with stout striated median seta. Peraeopods 5-7, basis regularly broadened, hind margin of peraeopod 5 with notch and surge seta; segments 4 & 5 slender, not shortened; segment 6, distal locking spine small to medium.

Epimeral plates 2-3 smooth below, hind corners subrectangular to rounded. Pleopods regular. Uropod 1, peduncle with strong posteromedial and posterolateral spines; rami longer than peduncles, each armed with marginal and one or more long strong apical spines. Uropod 2, outer ramus the shorter, with strong marginal and apical spines. Uropod 3 uniramous, ramus subequal to peduncle, both with strong apical and occasional posterior marginal spine(s).

Telson lobes short, broad, margins unarmed.

Female: Gnathopods 1 & 2 subsimilar, regular, 2 slightly larger; basal hydrodynamic lobes medium. Preamplexing notch regular, lacking unguisial groove or locking slit, but having very narrow anterior aperture; lower poster lobe of peraeon 2 large. Brood plate 2 medium large, spade-shaped, acute, margins with numerous very short, hook-tipped setae.

Etymology: The patronym honours the perceptive primary work of Dr. Cristiana Serejo, Museo Nacional de Brasil, in defining this hyalid species complex, and her continuing significant contributions to knowledge of the Brazilian amphipod fauna.

Distributional ecology: Composite species are recorded from surf beaches of the coast of Brazil and tropical and warm-temperate eastern N. & S. Atlantic shores, from the coast of Africa and offshore islands, including Madeira, north to the Basque coast of Spain & Bay of Biscay (Serejo 2001). Among green algal masses, from mid to low tide levels; not recorded from the Mediterranean or Caribbean Seas.

Remarks. The *Serejohyale* group is endemic to rocky surf beaches of the North and South Atlantic. The medium-sized animals are closest to species of *Apohyale* but are distinguished mainly by shallow coxal plates, a very large, irregularly palmate gnathopod 2 (male) and strong distomedial and distolateral spines on the peduncle of uropod 1. The form of the propod of gnathopod 2 (male) with its excavate palm and elongate dactyl, appears grossly similar to that of the talitrid *Orchestia kosswigi* Ruffo, 1951. A comparative table of character states of component species of *Serejohyale* is provided by Serejo (2001: p. 491).

Ruffohyale n. g.

Hyale Rathke 1837 (part);—Ruffo 1958: 50;—Barnard & Barnard 1983: 162;—Barnard & Karaman 1991: 367.

Type species: *Hyale milloti* Ruffo, 1958 (present designation) (see fig. 57, p. 120).

Species: *Ruffohyale incerta* (Chevreux, 1913); *R. jeanneli* (Chevreux, 1913); *H. milloti* (Ruffo, 1958).

Diagnosis: Body small to medium, smooth. Pigmented eyes lacking. Antennae medium, slender, subequal in length. Antenna 1, peduncular segments 2 and 3 not shortened; flagellum slender. Antenna 2, peduncular segment 4 and 5 subequal, medium stout flagellum short, segments may have tufts of fine setae.

Upper and lower lips regular. Mandible, left lacinia 6-dentate, spine row with 3 blades. Maxilla 1, inner plate short, apical setae long; palp medium short, 1-segmented. Maxilla 2, inner plate with single marginal plumose setae. Maxilliped regular, inner plate narrow; palp segments 1-3 stout, segment 1 relatively large; dactyl regular, unguis short.

Coxal plates 1-4 regular. Coxa 1 slightly broadened, with weak posterior marginal cusp. Coxae 2-4 with small posterior marginal cusps. Coxa 5 shallowly aequilobate. Coxae 6 and 7 shallowly posterolobate.

Gnathopod 1 little or not sexually dimorphic; hydrodynamic lobe of basis small; carpus elongate, with broad shallow lobe; propod (♂) deep, shorter than carpus, lacking mediofacial guiding spine; dactyl simple, not exceeding palm. Gnathopod 2, basis with medium hydrodynamic lobe; carpus lacking posterior lobe; propod large deep, palm regular, oblique; dactyl short.

Peraeopod 3-7 slender, dactyls very short with weak inner marginal seta; bases regularly broad, hind margins rounded, lacking notch and surge seta; segments 4 and 5 slender, segment 6 lacking inner marginal clasping spine.

Epimeral plates 2 and 3 subrectangular, hind corner squared. Uropod 1, peduncle longer than rami, distolateral and distomedial spines small; rami with short to medium marginal and apical spines. Uropod 2 short, stout, peduncle and rami regularly spinose, outer ramus the shorter. Uropod 3, peduncle short, very deep, lacking distal spine(s); ramus very short.

Telson lobes elongate triangular, margins smooth.

Female: Gnathopod 1 similar in form to that of the male, but weaker, with relatively short carpus, and hind margin of the coxa with shelf, but lacking a distinct posterior marginal cusp. Gnathopod 2 strong; propod may be large and powerful as in the male *(R. jeanneli)*.

Brood lamellae elongate, medium broad, apex rounded; brood setae medium long, with curled tips. Preamplexing notch shallow, obtuse, with short unguisial groove and anterior accessory slit; posteroventral lobe of peraeon 2 shallow, anterior margin slightly convex (*R. jeanneli*, fig. 58).

Etymology: The genus is named in honour of Dr. Sandro Ruffo who first suggested (1958, p. 50) that this morphologically distinctive complex of anophthalmic freshwater species of *Hyale* might "justifier la séparation .... en un genre différent". It also recognizes Dr. Ruffo's outstanding lifetime contributions to advancement of systematic knowledge of the Amphipoda.

Distributional Ecology:All species of this group are anophthalmic and occur in phreatic or subterranean parts of freshwater streams in near-African continental islands of the western Pacific Ocean. *Ruffohyale milloti* was collected in moss on rocks and under stones in waterfalls at 400 m a.s.l. on the island of Moheli, in the Comores Islands, off Madagascar. *H. jeanneli* and *H. incerta* were taken in wells (Shimoni Grotto) and small lakes of Zanzibar.

Remarks: The mouthparts *R. milloti* were not actually described or figured in Dr. Ruffo's original treatise (1958, p. 47). An apparent lack of diagnostic character states of mouthparts of the type species might lessen the reliability of generic diagnosis based on other character states alone. However, the mouthparts of the closely similar species, *R. jeanneli*, were figured and described by Chevreux (1913) (Fig. 58), to which those of *R. milloti* conformed "parfaitment" (Ruffo, loc. cit.). Accordingly, character states of the mouthparts of *R. jeanelli* are here incorporated in the generic diagnosis of *Ruffohyale*.

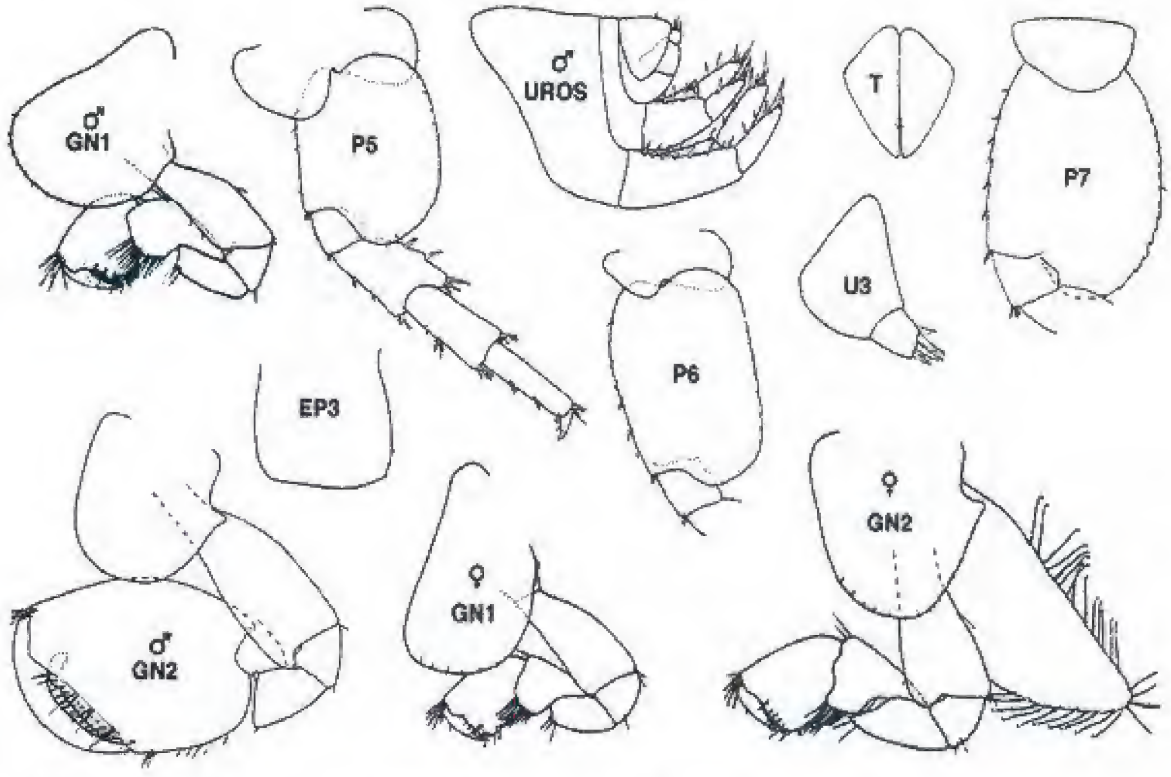

Fig. 57. *Ruffohyale milloti* (Ruffo, 1958). Male (4.5 mm); female ov (3.5 mm). Madagascar. (modified from Ruffo, 1958).

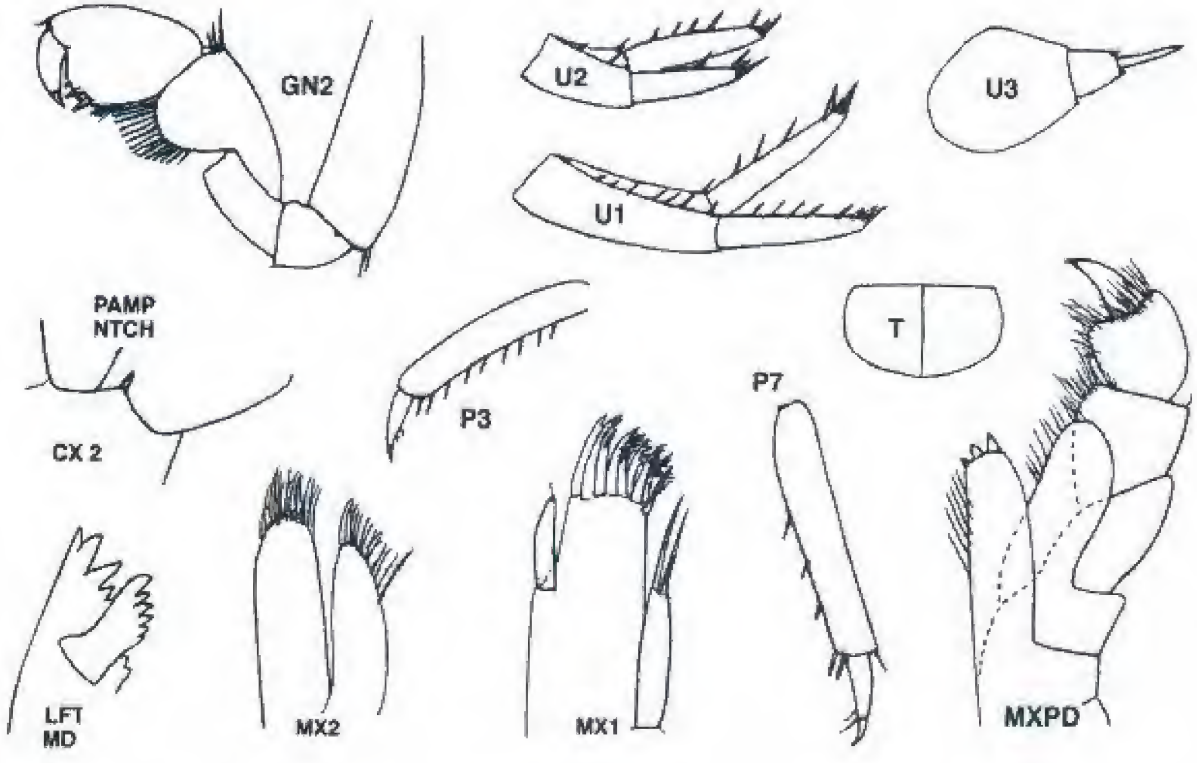

Fig. 58. *Ruffohyale jeanneli* (Chevreux, 1913). Female ov (9.0 mm). Subterranean lake, Kufile, Zanzibar (CMN collections).

The close morphological similarity of *Ruffohyale* to saltatory subgroups of *Hyale* sens. lat. suggests that these freshwater forms may have evolved from local seashore species ancestral to genus *Apohyale*, perhaps during the late Cretaceous, before Madagascar split off from the African continent (Bousfield 1984). Possibly near-contemporaneously, members of the freshwater neotropical genus *Hyalella* may have evolved from ancestral marine members of an *Allorchestes*-like ancestor within the family Hyalellidae (Bousfield 1996).

Ruffohyale jeanneli (Chevreux)
(Fig. 58)

Hyale jeanneli Chevreux, 1913: 18, fig. 3;—Barnard & Barnard 1983: 716;—Barnard & Karaman 1991:369.

Material examined:
Subterranean lake, Kufile, Zanzibar, J. Omer-Cooper coll., Sept. 2, 1955 - 5 ♂♂, 3 ♀♀ov. , CMNC 2002-0072.

Diagnosis: Male (to 14 mm). Antennae medium long, subequal. Antenna 1, flagellum 18-segmented. Mandibular left lacinia 6 1/2 dentate. Gnathopod 2, propod large, palm oblique, lined with fine spines, dactyl slender. Uropod 1, peduncle and outer ramus with 5-6 marginal spines. Uropod 3 , peduncle stout, ramus very short.

Female ov. (to 9.0 mm). Gnathopod 2 powerfully subchelate, as in male. Preamplexing notch shallowly obtuse; unguisial groove very short.

Subfamily Kuriinae new status

Kuriidae Barnard, 1964: 66. Barnard & Karaman 1991:403.

Type Genus: *Kuria* Walker & Scott, 1903: 228.

Genera: *Micropythia* Krapp-Schickel, 1974.

Diagnosis: Body small, mid-dorsally carinated; surfaces finely pilose. Urosome segments may be fused. Antennae short, subequal.

Mandible regular, lacinia 4-5 dentate. Maxilla 1, palp 1-segmented, medium. Maxilliped, palp slender, reduced; dactyl short, unguis attenuated.

Coxal plates deep; coxae 2 and 3 each with sharp posterior marginal cusp, lower margins weakly crenulate.

Gnathopods slender, not sexually dimorphic; basal and ischial segments lacking hydrodynamic lobes (both sexes) (fig. 59); carpus and propod shallow, elongate; dactyl distinctly overlapping palm.

Peraeopods 5 -7, bases broad, hind margin strongly convex, crenulate; segment 4 strongly broadened and lobate posteriorly; segment 5 short; dactyls strong.

Uropods 1 & 2, peduncle, distolateral and distomedial spines weak. Uropod 3 uniramous, ramus shorter than peduncle, with apical spines only. Telson lobes medium, triangular, with apical seta(e).

Female: Brood plates distally rounded, marginal setae long. Preamplexing notch undescribed, presumably lacking.

Remarks. The genus *Micropythia* is unique among hyalid amphipods in lacking sexually dimorphic gnathopods. However, *M. carinata* Bate has several character states in common with *Hyale pontica* Rathke, 1837, type species of family Hyalidae (see Bulycheva 1957: 90-91, fig. 30. These include (Fig. 59a, b): (1) body slightly or moderately mid-dorsally carinate; (2) maxilliped palp, distal segments weak, dactyl small, with slender elongate unguis; (3) gnathopod 1, dactyl overhangs short palm; (4) coxal plates 1 and 4 lack posterior marginal cusp; (5) peraeopods 5-7, hind margins of bases scalloped or crenulated; segment 4 broadened posterodistally; segment 5 short; dactyl large, simple; (6) uropod 1 lacking distal peduncular spines, rami each with long terminal spine; (7) uropod 3, ramus shorter than peduncle; (8) brood plate (gnathopod 2), ovate, with longish marginal setae.

In our opinion, resemblance of *Kuria longimanus* to *Micropythia carinata*, and to *Hyale pontica*, type of family Hyalidae, is suffiently strong in most of these character states as to preclude convergence or homoplasious similarity (Fig. 59). Family Kuriidae Barnard is apparently based on one species, *K. longimanus*, that can be included within the previously described family concept of Hyalidae. Its single unique character state (fused urosome segments) is not generally considered to be of family level significance and cannot therefore stand alone. With the concurrence of Dr. Krapp-Schickel we hereby relegate Barnard's initial concept to subfamily status within family Hyalidae. This action recognizes both taxonomic similarities and distinctiveness of *Kuria* and *Micropythia* to other genera within the family.

The original description and figures of *Kuria longimanus* did not include information on pleopods, brood plates, coxal gills, preamplexing notch, and some mouthparts. Moreover, the overlapping of coxal and basal plates appears incorrect (previously noted by Barnard 1969a) and posterior marginal cusps on some

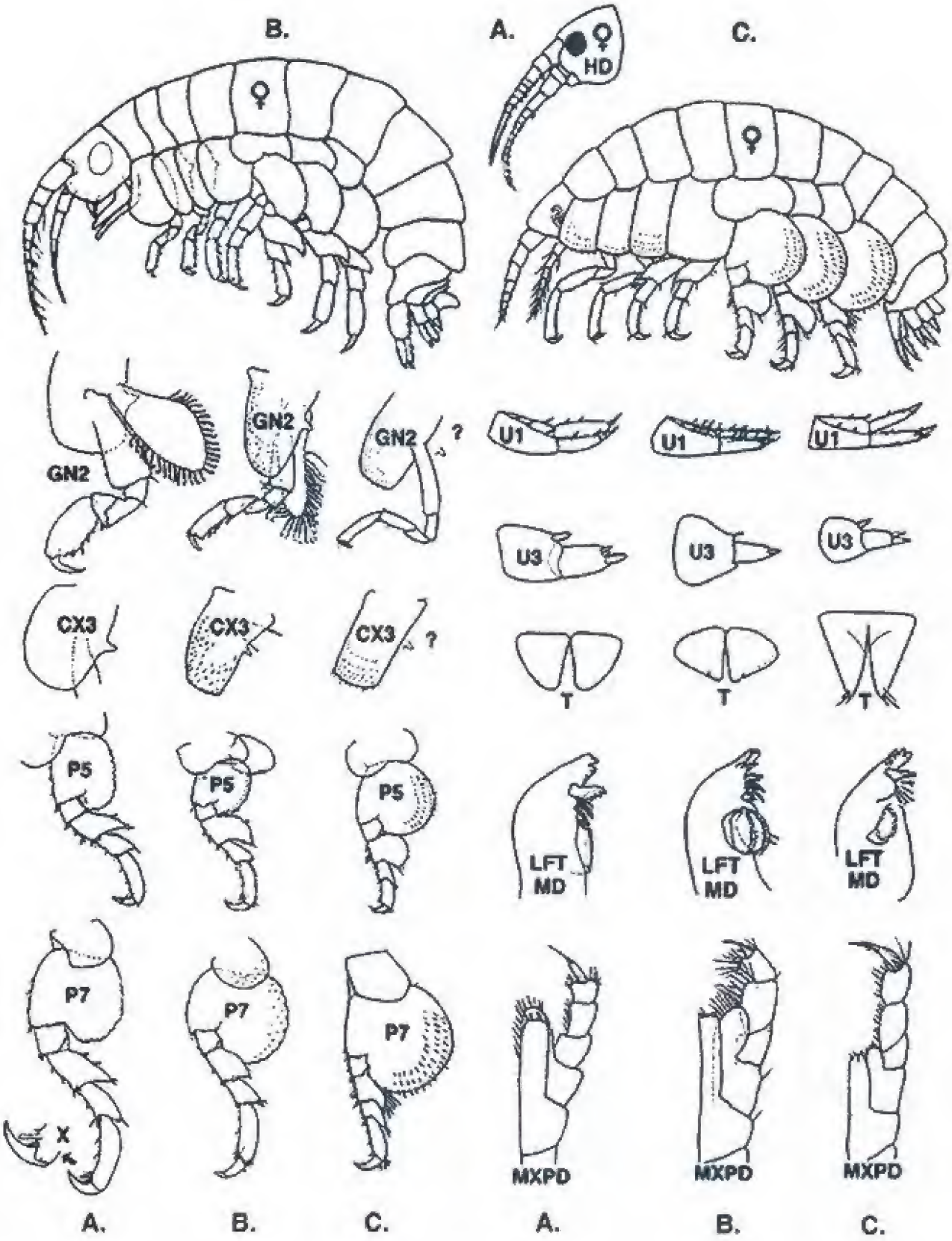

Fig. 59. Morphological comparison between hyalid subfamilies Hyalinae and Kuriinae: A. *Hyale pontica*; B. *Micropythia carinata*; C. *Kuria longimanus*. (modified from A. Krapp-Schickel & Bousfield 2002; B. Krapp-Schickel 1993; C. Walker & Scott 1903).

Key to genera of subfamily Kuriinae

1. Urosome segments fused; gnathopods 1 & 2, carpus and propods elongate, lengthof each > 3X depth; telson lobes narrowly triangular, longer than wide ..... *Kuria* Walker and Scott.
Urosome segments separate, regular; gnathopods 1 & 2, propod and carpus slender, length of each < 3X depth; telson lobes short, broadly triangular ..... *Micropythia* Krapp-Schickel.

anterior coxal plates may have been omitted. Cognizant of these descriptive limitations, and that the material of Walker & Scott (1903) cannot be located for redescription (Krapp-Schickel, pers. comm.), the present conclusions are tentative, pending acquisition of fresh material of *Kuria longimanus*. Thus *Micropythia carinata* appears similar to *Kuria*, but unlike all members of subfamilies Hyalinae and Hyachelinae, in lacking sexually dimorphic gnathopods, and preamplexing notch on peraeon 2 (female).

Structure of the coxal plates within subfamily Kuriinae is also morphologically distinct. Krapp-Schickel (1993: p. 741, fig. 507) noted in *Micropythia* that coxa 2 is marked by a blunt rounded prolongation anteroproximally along the insertion line. This coxal "hump" occurs in both sexes but is stronger in mature females and reaches halfway along the insertion margin of coxa 1. In addition, coxae 2 and 3 exhibit similar sharp posterior marginal prolongations or cusps. Krapp-Schickel (pers. comm.) suggests that coxae 2+3+4 may thereby act in concert as one plate. Moreover, the coxae are unusually large, masking most of the legs, and are inserted only half or less of their breadth at the body, the anterior half of each coxa being free. In the illustration of Krapp-Schickel (1993, fig. 507), coxae 1-3 (male) also bear an anteroproximal lobe that apparently slips under the anterior portion of the peraeon segment proper and presumably provides further rigidity to the plate assembly.

Hyacheliinae n. subfam.

Type genus: *Hyachelia* Barnard, 1967.

Diagnosis: Sexually dimorphic: ectoparasitic in the buccal cavity of marine tortoises. Body smooth, uncarinated. Eye large, lenticular, black. Antennae short, flagellum 8-9 segmented. Antenna 2, peduncular gland cone small, segments 4 and 5 swollen (male).

Mandibular left lacinia 4-5 dentate? Maxilla 1 palp very reduced (as in Hyalellidae). Maxilliped palp, plates slender; dactyl short, nail very small.

Coxae 1-4 large, deep, smoothly overlapping, hind margins lacking posterior marginal shelf and cusp. Coxae 5 anterolobate: coxae 6 & 7 posterolobate. Coxal gills sac-like, broadly cross-pleated.

Gnathopods strongly sexually dimorphic, typically hyalid in form. Hydrodynamic lobe of basal and ischial segments weak or lacking in gnathopod 1, weakly present in gnathopod 2 (both sexes). Carpus of gnathopod 2 (male) lacking posterior lobe.

Peraeopods very smooth, lacking marginal armature, distally weakly subcheliform, palm with short cuved spines; dactyl stout, striated.

Pleopods strongly natatory, rami elongate, fully plumose-setose. Uropods 1 and 2 strong; rami variously marginally setose, natatory; Uropod 3 minute, peduncle subtriangular, lacking rami. Telson fully bilobate, margins smooth.

Female: Gnathopods 1 and 2 subsimilar in size and form; carpal lobe slender; dactyl overlapping short palm. Brood plates elongate triangular, brood setae medium long, curl-tipped. Peraeon 2 with distinct subquadrate preamplexing notch, lacking unguisial groove; posteroventral lobe of peraeon 2 short, small rounded.

Distribution: Galapagos Islands, Eastern tropical Pacific; south of Dakar, eastern tropical Atlantic; on *Chelonia*.

Remarks: Uropods 1 and 2 appear to have become secondarily modied to form a powerful forward thrusting tail fan in which the bilobate telson remains as a possible steering mechanism. The coxal and basal plates of the peraeopods remain large, uniform, and smoothly overlapping, presumably hydrodynamically, and facilitating rapid swimming, as between host turtles. The pleopods are also exceptionally strongly natatory.

The peraeopods are unusually smooth, perhaps lessening irration of host buccal tissues. Amphipod ectoparasites of fishes within primitive superfamilies Lysianassoidea (e.g., Opisidae, Trischizostomatidae) and Pardaliscoidea (e.g., *Halice*), have a similarly laterally compressed natatory body form. In the more advanced Iphimedioidea (e.g., Lafystiidae), the body form is more dorsoventrally depressed, and less strongly natatory. In the highly advanced Caprellidea (family Cyamidae) that are ectoparasitic on marine mammals,

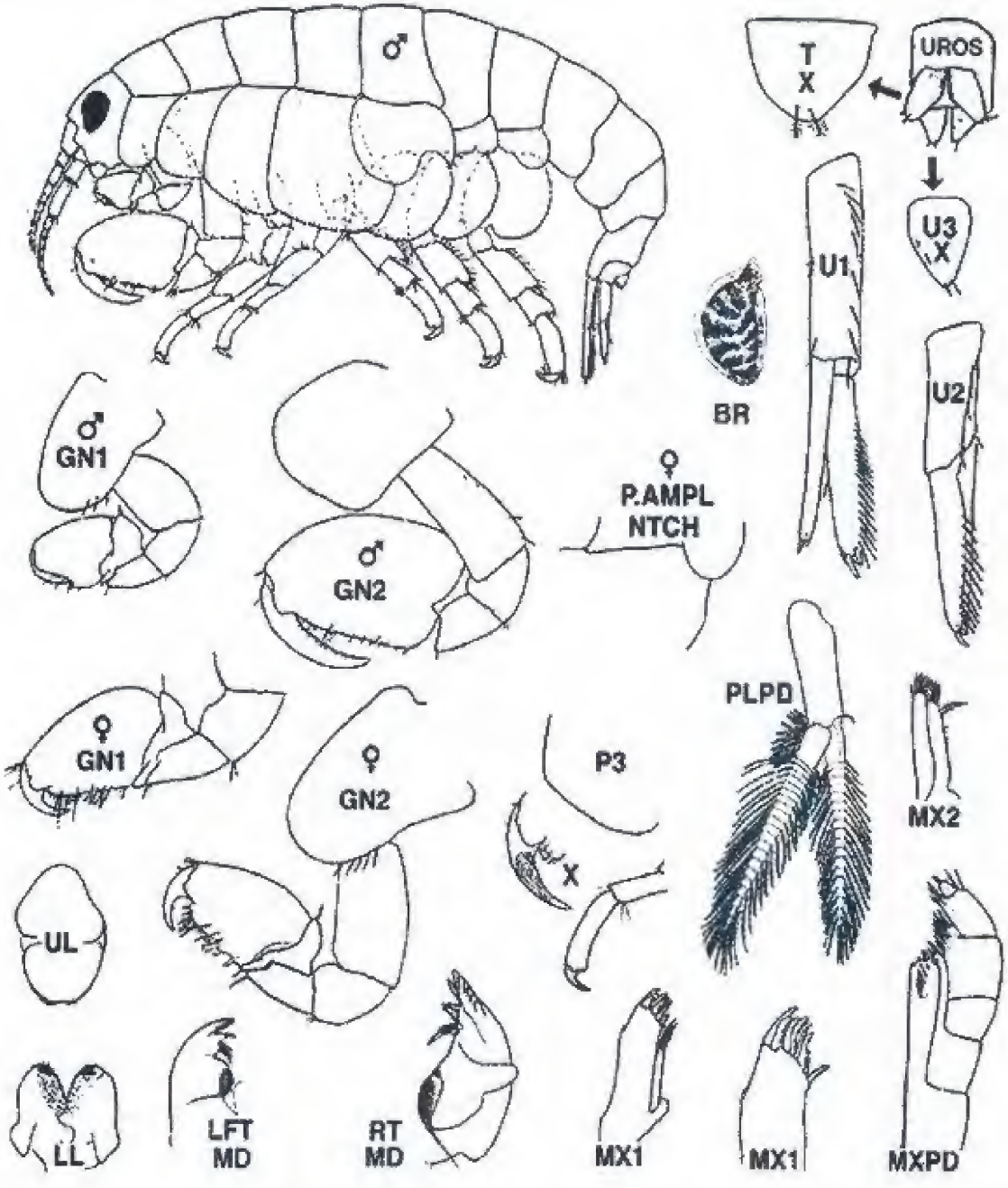

Fig. 60. *Hyachelia tortugae* Barnard, 1967. Male (7.1 mm); female ov (6.9 mm). Dry Tortugas. (modified from Barnard, 1967; preamplexing notch courtesy C. Serejo)

the body form is highly depressed dorsoventrally and non-natatory. However, limb segments are secondarily hydrodynamically lobate presumably to streamline the surfaces exposed to strong water currents induced by the rapidly swimming host. *Hyachelia*, *Apohyale*, and *Serejohyale* may have diverged from an immediate common shore-dwelling ancestor. Vacating of intertidal habitats for a epiparasitic life style on marine turtles may have coincided with early stages of broadening of the Tethyan-Atlantic ocean.

***Hyachelia* Barnard**

Hyachelia J. L. Barnard, 1967: 120 figs 1-4.

Type species: *Hyachelia tortugae* Barnard, 1967, original designation and monotypy.

Species: *Hyachelia tortugae* Barnard, 1967: 120, figs. 1-4;—Ruffo 1975: 482;—Barnard & Karaman, 1991: 123.

Diagnosis: see Barnard & Karaman 1991: 122. and Fig. 60, p. 124.

Remarks: This aberrant ectoparasitic hyalid has been placed within the Ceinidae by Barnard & Karaman (1991). However *Hyachelia tortugae* bears little or no resemblance to *Ceina egregia* (Chilton,1883), the type species of family Ceinidae Barnard, 1972.

Morphological similarities with the genus *Hyale* are much more pronounced, especially in uropod 3 and telson. Major differences with *Hyale*, however, lie in uropods 1 and 2, the rami of which are large, flattened, each with inner margin of one ramus serially spinose.

Hyachelia is here treated as a unique subfamily member within family Hyalidae.

Drs. Krapp-Schickel and Serejo very recently found a preamplexing notch in mature female specimens of *Hyachelia tortugae* (Fig. 60), strengthening the present decision to remove the genus from family Ceinidae and erect for it a new subfamily within family Hyalidae. It apparently occurs also in families Hyalellidae and Dogielinotidae and, in modified form, in family Najnidae. However, the preamplexing notch has not yet been found even within the most primitive "palustral" genera of family Talitridae (e.g., *Eorchestia*, *Protorchestia*). It would appear, therefore, that this feature occurs in talitroidean groups that preamplex aquatically and not terrestrially.

DISCUSSION

Systematic Reorganization of family Hyalidae.

The recent increase in knowledge of the systematics of hyalid amphipods, now numbering ~ 110 described species, necessitated further reorganization at subfamily and genus levels. In brief review, Bulycheva (1957) had regrouped species formerly assigned to family Talitridae sens. lat.,within family Talitridae Rafinesque, 1815, and two new families, Hyalidae and Hyalellidae. This complex was combined with several related but somewhat aberrant family-level taxa, within her newly proposed superfamily concept, Talitroidea. At that time, family Hyalidae encompassed about 35 species, almost entirely littoral marine, in 5 genera (*Hyale* Rathke, 1837 sens. lat.; *Parhyale* Stebbing, 1899; *Allorchestes* Dana, 1849; *Ceina* Della Valle, 1893; and *Najna* Derzhavin, 1937). The semiterrestrial and terrestrial species, by far the largest number of species, were retained within family Talitridae (Bousfield 1984).

Subsequent growth of family Hyalidae has been rapid, summarized in part by Barnard & Karaman (1991). *Ceina* had been transferred to family Ceinidae and *Najna* to family Najnidae by Barnard (1972), and *Allorchestes* to Hyalellidae by Hendrycks & Bousfield (2001), However, Hyalidae now included *Lelehua* Barnard,1970, *Neobule* Haswell, 1879, *Micropythia* Krapp-Schickel, 1976, and *Parallorchestes* Shoemaker, 1941 was separated from *Parhyale* Stebbing, 1899. As noted elsewhere in this study, three littoral marine genera (*Allorchestes, Parhyalella,* and *Insula)* had been more suitably transferred to family Hyalellidae.

Recognition of broader diversity within hyalids of the Canadian Pacific coast of North America had been initiated by Bousfield (1981). Numerous regional species, mostly new to science, could be assigned to *Parallorchestes* Shoemaker, or to the unwieldy genus *Hyale* Rathke sens. lat. Phenetic cluster analysis yielded several species groups that, especially within *Hyale*, could be recognized informally at new generic and subgeneric levels. Several species names that were intended to be given full taxonomic treatment in a companion study, were illustrated more or less fully. However, the new taxa were not then fully described, nor type material and type localities designated because of the abrupt discontinuance of the intended taxonomic outlet. Some names, newly proposed but not formally described at that time, remained taxonomically unavailable (*nomina nuda)*. Some have been replaced in this study, but all are now validated by the present full descriptive accounts (ICZN 1985).

Extension of preliminary analysis of the N. American Pacific groupings to the far more extensive worldwide hyalid fauna, has here revealed a broad consistency of applicability and thus legitimacy of character states selected (Figs. 1-15). Thus, as indicated in the phenogram of 20 generic character state similarities (Fig. 61), the present world fauna of ~110 described hyalid species can be separated broadly into two major groupings: (1) to the left, is a cluster of four relatively primitive (P.A. indices of 4 to 14), mainly low-intertidal and subtidal, natatory genera (including *Protohyale* with 4 subgenera); (2) to the right, is a grouping of five generally more advanced genera (P. A. Indices of 10 to 20) that are more intertidal in vertical station, and saltatory in locomotory behaviour. The genus *Hyale* Rathke sens. str., as noted above (p. 100), is somewhat intermediate between the two in possessing character states that are mainly natatory and plesiomorphic, but also a few that appear saltatory and apomorphic, and one (unique among hyalid genera) that is apparently specialized for preamplexus in a highly lotic environment.

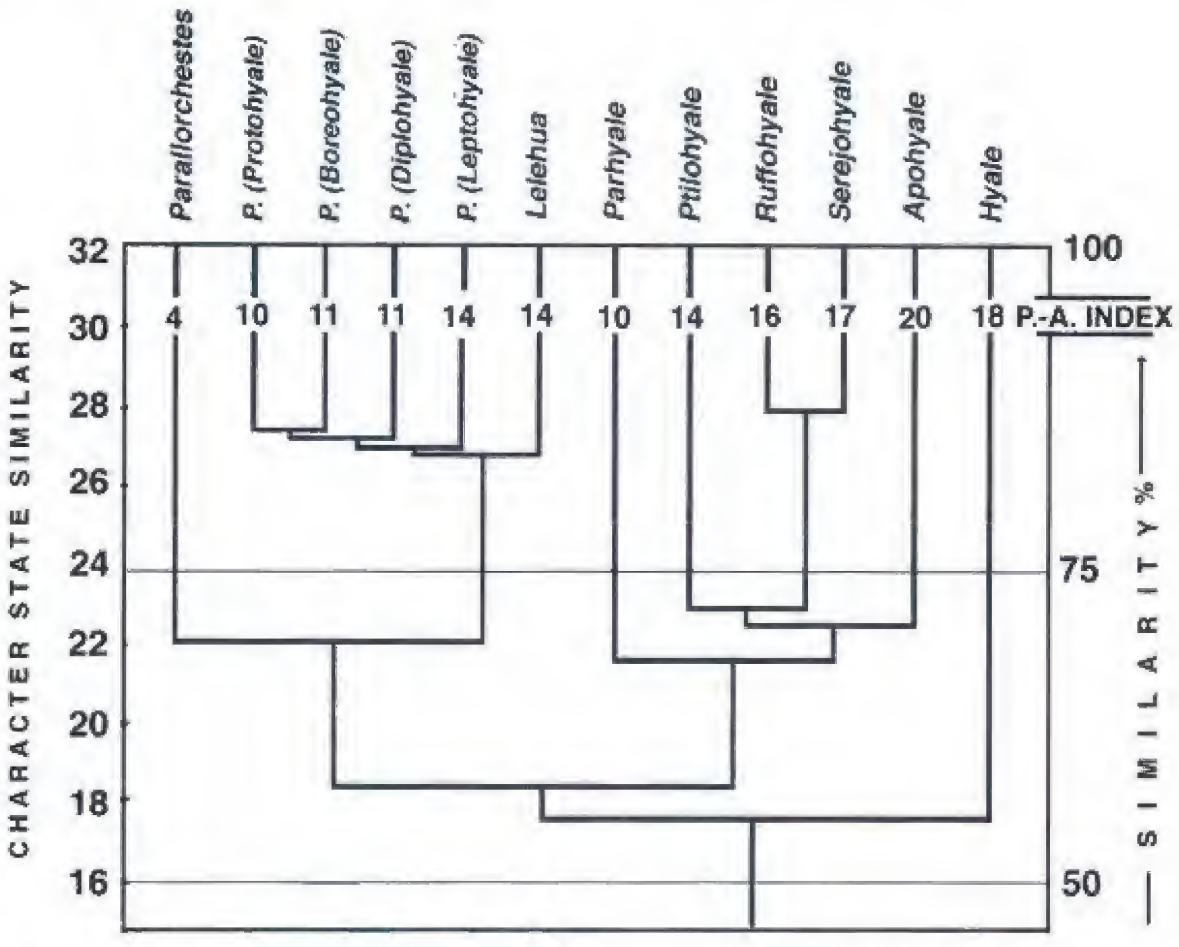

Fig. 61. Phenogram of morphological similarities and possible phyletic relationships within world genera of Hyalinae (excluding enigmatic genus *Neobule*).

Species of the natatory group tend to have well developed hydrodynamic lobes on the basis and/or ischium of gnathopods 1 & 2 (especially in the male), a strongly developed distolateral peduncular spine on uropod 1, and large subovate distally rounded brood plates with elongate marginal setae, but the posterior margins of coxae 1-4 are generally non-cuspate. In peraeopods 5-7, the posterior margins of the bases tend to be crenulated, with conspicuous notch and surge seta, one or two clasping spines are present distally on segment 6, and dactyls are relatively large and simple with small interior marginal seta. This relative primitive natatory group encompasses slightly more than half the described species of Hyalidae, and species of all but *Parallorchestes* and subgenus *Boreohyale* tend to be small in size and tropical-warm-temperate in distribution. In the most primitive genus *Parallorchestes* (P. A. Index = 4), the palp of maxilla 1 is uniquely 2-segmented, the inner ramus of uropod 3 is distinct, and the telson is spinose apically.

The five genera to the right (Fig. 61) are relatively advanced. All but *Ruffohyale* are more or less intertidal, amphibious, and capable of saltation in air. They have posteriorly cuspate coxal plates, and the brood plate of gnathopod 2 is large and elongate, often spade-shaped, and the margins lined with very numerous, short, hook-tipped setae. Conversely they are characterized by weakly developed gnathopodal hydrodynamic lobes, peraeopodal notch and surge setae, distal clasping spine, small dactyls, and small distolateral spine of uropod 1. Of these five genera, the more primitive *Parhyale* and *Ptilohyale* have a small inner ramus on uropod 3, distinct or variously fused to the peduncle. *Parhyale* is also distinguished by a strongly developed cusp on the posterior medial margin of coxa 4, and rarely by setae on peduncle 4 of antenna 2, both lacking in *Ptilohyale*. The advanced genera *Apohyale* and *Ruffohyale* lack pronounced distal peduncular spines both of which are strongly developed in *Serejohyale*. Saltatory ability is marked in *Ptilohyale* and especially

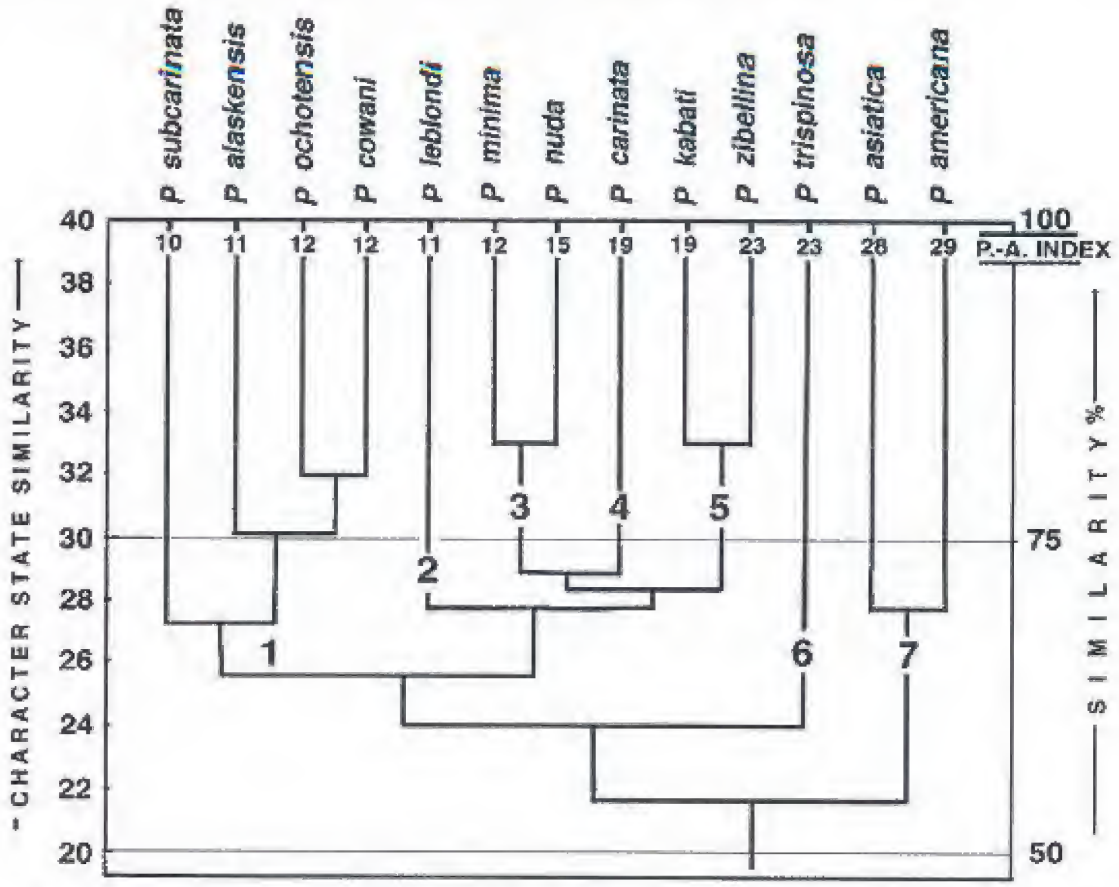

Fig. 62. Phenogram of morphological similarities and suggested phyletic relationships within North Pacific species of *Parallorchestes*.

strong in *Apohyale* and *Serejohyale*.

As indicated in the phenogram of 20 generic character state similarities (Fig. 62), the 13 described species of *Parallorchestes* can be assigned broadly into two major groupings and 7 minor components. The *ochotensis* group (1), on the left, encompasses 4 relatively primitive (P. A. indices of 10-12) carinated subarctic species. In the centre is a loosely related group of six species of which (3) (*P. minima* and *P. nuda*) and (5) (*P. kabatai* and *P. zibellina*) appear to form natural species pairs.

On the extreme right (7) is the advanced species pair *P. asiatica* and *P. americana* (P. A. indices of 28, 29), whose similarities were detailed by Tzvetkova (1990). In advanced *species P. trispinosa* (6), the dactyl tips of gnathopod 1 (♂) are bifid (cf. *Allorchestes*), and the ramus of uropod 3 has three marginal spine groups.

Results of phenetic cluster analysis of subgeneric and species components of genus *Prothohyale*, based on 17 paired generic character states, are graphed in fig. 63 (characters and states as outlined in Figs. 1-3, etc.).

Species of subgenus *Boreohyale* cluster in two main subgroups on the left. The seven regional species exhibit an unreduced peduncular segment 2 of antenna 1, the basal hydrodynamic lobe of gnathopod 1 is little developed or lacking (males), and well developed on the basis of gnathopod 2 in males only. Antennal flagella tend to be elongate and the mandibular left lacinia is typically 5-dentate. Component species are mainly cold-temperate in distribution (Table III).

Species of the nominate subgenus *Protohyale* cluster in one main subgroup of six species to the right. The subgenus, exemplified by the type species *P. (P.) frequens* (Stout), shows reduction of peduncular segment 2 of antenna 1, and development of hydrodynamic lobes on the basis of gnathopods 1 & 2 of females, as well as strong development on both basis and ischium of males. To the extreme right is a somewhat aberrent member of the subgenus, *P. (P.) guasave*, a member of the advanced *P. macrodactyla* subgroup, having a relatively high P.-A. index of 23. This sub-group is distinguished by the specialized form of gnathopods 1 & 2 (♂) (Fig. 41). Counterpart species of this subgroup occur in Hawaii and Japan (Table IV). Component species are tropical and warm-temperate in distribution (Table III).

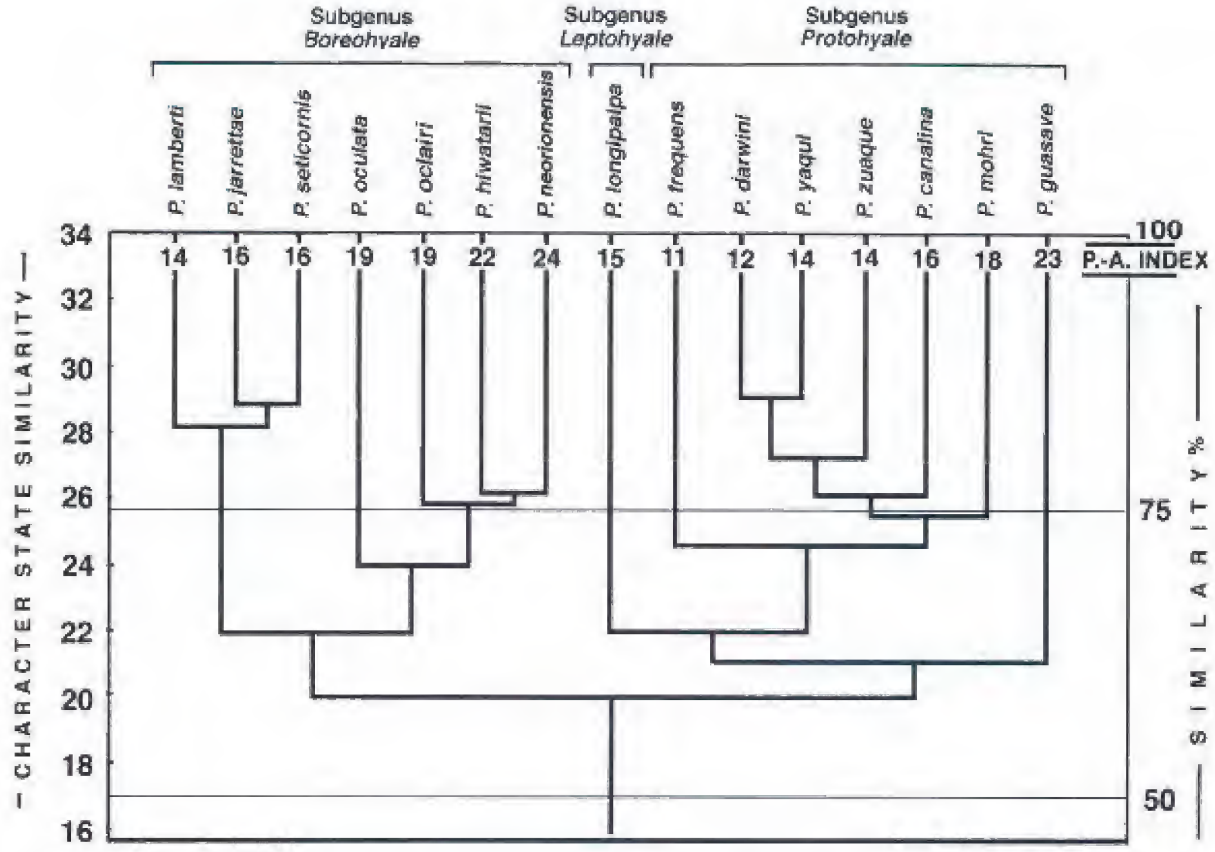

Fig. 63. Phenogram of morphological similarities and possible phyletic relationships within genera and subgenera of genus *Protohyale* on the North American Pacific coast.

Occupying a central position on the graph is the monotypic subgenus *Leptohyale*, the sole species of which *(L. longipalpa)* has a low to intermediate P.-A. index of 15. The species differs from other protohyalids in a small eye, 7-8 dentate left lacinia, strongly sexually dimorphic maxilliped palp (distal segments elongate in males), and markedly differing size and stoutness of peraeopods 3-4 vs. peraeopods 5-7. This subgenus is apparently endemic to the North American Pacific region wherein its single species occurs infrequently and discontinuously (Fig. 64C)

Detailed distribution of species representative of genera and subgenera on the Pacific coast of North America are portrayed in Fig. 64. Wide-ranging species (occurring in 4 or more biogeographic subzones of Table III) are actually in the minority (11/29 species). A few are species of the natator group (e.g., *Parallorchestes cowani* and *P. (Boreohyale) seticornis* (Fig. 64 A,B). Several natator species including *Parallorchestes alaskensis, P. nuda, P. trispinosa, P. (Boreohyale) hiwatarii* and *P. (B). oclairi* are restricted to one or two zones, even where field collecting has been relatively intensive. *Leptohyale longipalpa* is somewhat intermediate; it ranges narrowly from part of one boreal zone, through two zones, to the middle part of a fourth boreal zone (Fig. 64C).

By contrast, within the saltator genera all four North American species of genus *Ptilohyale* and *Apohyale* occur across five or more biogeographic subzones. The less aquatic and higher level intertidal species are presumably exposed to greater ranges and more rapid changes of physical factors than aquatic species. Species of family Talitridae (e.g.,*Traskorchestia traskiana*), living at and above the HW level, exhibit even wider regional distributions (Bousfield 1982). *Ptilohyale plumulosa* occurs in brackish pools and estuaries that are moderately warm in summer and free of heavy winter icing but may undergo relatively rapid diurnal changes. *Apohyale pugettensis* apparently thrives in spray pools, at and above the HW level, that are exposed to short- and long-term extreme changes of temperature and salinity. Thus, greater ecological "hardiness" is a probable factor contributing to the generally wider ranges of saltatory versus natatory hyalid species.

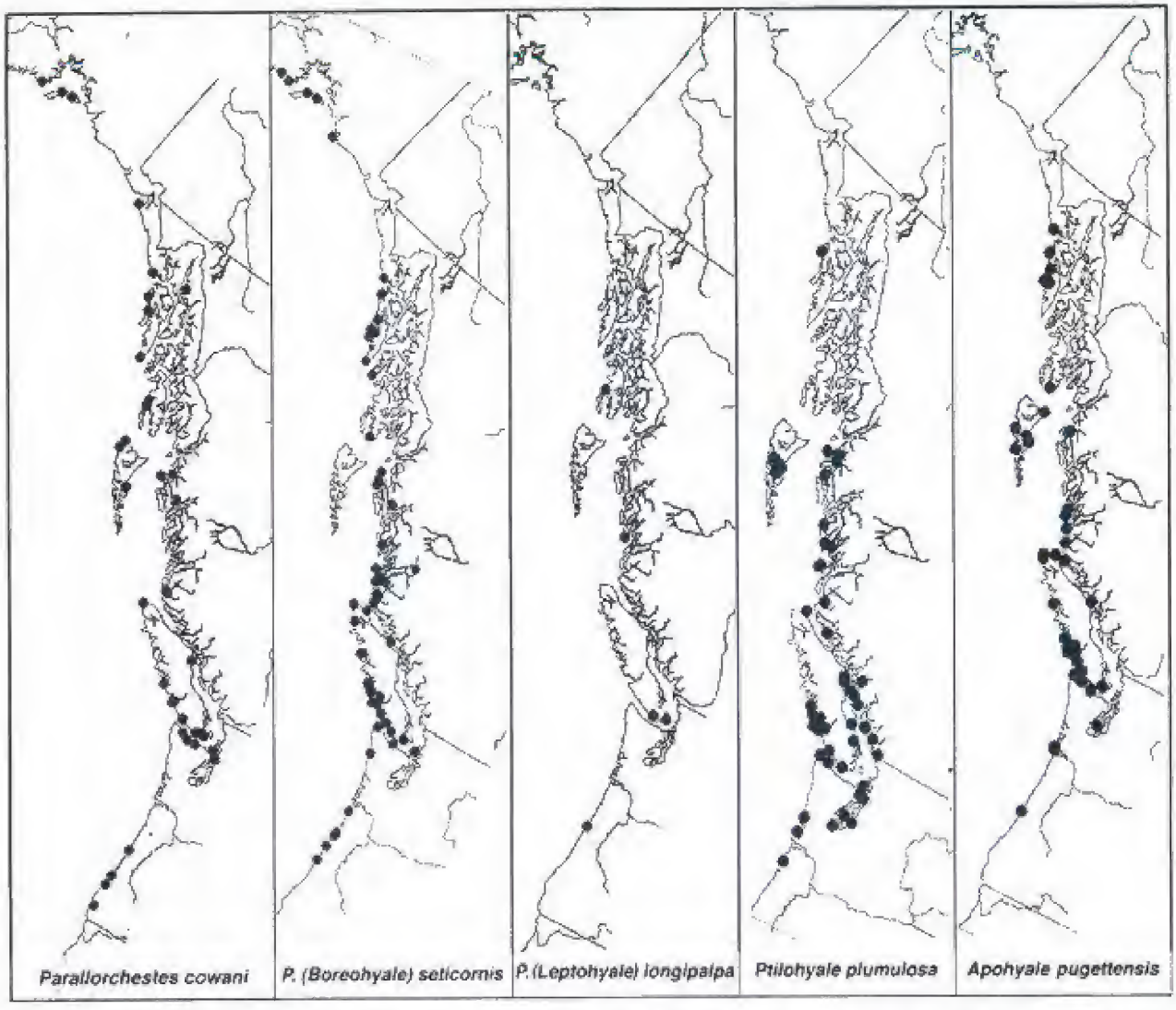

Fig. 64. Distribution of representative species of hyalid genera on the North American Pacific coast. **A**. *Parallorchestes cowani* n. sp; **B**. *P. (Boreohyale) seticornis* n. sp; **C**. *P.(Leptohyale) longipalpa* n.sp. **D**. *Ptilohyale plumulosa* (Stimpson); **E**. *Apohyale pugettensis* (Dana).

Biogeographical Analysis.

The distribution of 41 described species of family Hyalidae in the North Pacific Basin (excluding the central Hawaiian archipelago) is represented in Table III. Some 30 species of primitive natators (swimmers) are encompassed within 3 genera and 3 subgenera, and 11 species of advanced saltators (jumpers) are contained in only 3 genera . The number of described species in the eastern N. Pacific is now 29, about twice the number (14) known from the western N. Pacific. These ratios may soon change since Dr. Hiwatari is currently describing a number of new, mainly natatory taxa from Japanese coastal waters. The eastern Pacific total combines 25 natators and 4 saltators; in the western Pacific, 7 natators and 7 saltators. In balance, therefore, the eastern Pacific has a higher proportion of primitive natators whereas the western Pacific has relatively more advanced saltators.

A more detailed examination of natators reveals that 24 species (in 2 genera and 3 subgenera) occur in the east, but only 7 species in 3 genera and 2 subgenera are known from the western N Pacific. The numbers for east and west total more than 30 because a single species (*Parallorchestes ochotensis*) has been recorded from both regions. Within *Parallorchestes*, all 13 species are subarctic and boreal, extending south to the northern Sea of Japan Sea in the west, and central California in the east. None occur in subtropical Hawaii. Similarly within subgenus *Boreohyale*, all species are cold-temperate and range south to the Sea of Japan in the west, and from Alaska to central California in the east. Again, none occur in Hawaii. In the east, several species of natators (e.g., *Parallorchestes richardsoni, P. (Boreohyale) oclairae*) show quite re-

Table III. Distribution of subfamily Hyalinae in the North Pacific coastal continental region. (Exclusive of Hawaiian and central North Pacific islands).

TAXON	BIOGEOGRAPHIC ZONES									
	1	2	3	4	5	6	7	8	9	10
Parallorchestes Shoemaker										
ochotensis (Brandt)		x	X	X						
zibellini (Derzhavin)		X	X							
asiatica Tzvetkova			X							
alaskensis n. sp.			X							
carinata n. sp.			X	X						
cowani n. sp.			X	X	X	X	X	X	?	
americana Bousfield			X	X	X	X	X	x		
kabatai n. sp.			X	X	X	X	x?			
minima n. sp.					X					
subcarinata n. sp.					X	X				
nuda n. sp.						X				
trispinosa n. sp.						X				
leblondi n. sp.						X	X			
Protohyale n. g.										
P. (Boreohyale) n. subg.										
pumila (Hiwatari & Kajihara)		X								
sp.1 (= *schmidti* Iwasa)		X								
lamberti n. sp.					X	X	X	X		
jarrettae n. sp.					X	X	X	X		
seticornis n. sp.					X	X	X	X		
hiwatarii n. sp.							X			
neorionensis n. sp.							X			
oculata n. sp.							X	X		
oclairi n. sp.							X	X		
P. (Leptohyale) longipalpa n. sp.					X	X	X	X		
P. (Protohyale) n. subg.										
corallinicola (Hirayama)	X									
frequens (Stout)									X	?
mohri n. sp.									X	
yaqui (Barnard)									X	X
canalina (Barnard)									X	X
guasave (Barnard)										X
Lelehua J. L. Barnard										
ishigaki (Hirayama)	X									
Parhyale Stebbing										
hawaiensis (Dana)	X									
iwasai (Shoemaker)	X									
Ptilohyale n. g.										
ptiloceros (Derzhavin)		X								
barbicornis (Hiwat. & Kajih.)		X								
plumulosa (Stimpson)					X	X	X	X	X	x
Apohyale n. g.										
bassargini (Derzhavin)		X								
punctata (Hiwatari & Kajihara)		X								
uragensis (Hiwat. & Kajih.)	x?	X								
anceps (J. L. Barnard)				X	X	X	X	X	x?	
pugettensis (Dana)				X	X	X	X	X	?	
californica (J. L. Barnard)					x	X	X	X	X	X

Biogeographic Zones: **1.** S. China Sea; **2.** Sea of Japan; **3.** Sea of Okhotsk & W. Bering Sea; **4.** E. Bering sea & Aleutians; **5.** Southeastern Alaska; **6.** Northern B. C.; **7.** Southern B. C.: **8.** Washington-Oregon to Central California; **9.** Southern California; **10.** Baja California. (**Natator** species are above, **saltator** species below, the double line).

Table IV. Genera and subgenera of Hyalidae and their counterpart species in Eastern, Central, and Western North Pacific Regions.

Pacific North America	Hawaiian Archipelago	Japan & Russia
A. Natatory (non-cuspate) spp.		
Parallorchestes cowani n. sp	–	*Parallorchestes ochotensis* (Brandt)
P. americana Bousfield	–	*P. asiatica* Tzvetkova.
P. kabatai n. sp.	–	*P. zibbelina* (Derzhavin)
Protohyale (Boreohyale) lamberti n. sp.	–	*P. (Boreohyale) pumila* (H. & K.)
	–	*P. (Boreohyale)* sp. (Hiwatari, i.p.)
	–	*P. (Boreohyale)* sp. (= *P. dollfusi* Bulycheva)
P. (Protohyale) frequens (Stout, 1913)	*P. (Protohyale) affinis* (Chevreux,) (Barnard 1965, 1970)	*P. (Protohyale) affinis* (Chevreux)
several spp. (Baja California)	*P. (Protohyale)* sp (c.f. *rubra*) (Barnard, 1970).	*P. (Protohyale) corallinicola* (Hirayama); several other small spp. (Hiwatari, i. p.)
–		
–	*P. (Protohyale) laie* Barnard, 1970)	–
macrodactyla subgroup	*macrodactyla* subgroup	*macrodactyla* subgroup
P. (Protohyale) zuaque (J. L. Barnard, 1979)	*P. (Protohyale) honoluluensis* (Schellenberg); (Barnard, 1979b)	*P. (Protohyale) honoluluensis* (Schellenberg, 1938)
–	–	*P. (Diplohyale) didendactyla* (Hirayama)
–	*Lelehua waimea* (Barnard)	*Lelehua ishigakiensis* (Hirayama)
B. Saltatory (cuspate) species		
–	*Parhyale hawaiensis* (Dana)	*Parhyale hawaiensis* (Dana)
–	*P. inyacka* K. H. Barnard	*Parhyale iwasai* Shoemaker
Ptilohyale plumulosa (Stimpson)	*Ptilohyale iole* (Barnard)	*Ptilohyale barbicornis* (H.& K.)
	–	*Ptiloh. ptiloceros* (Derzhavin)
Apohyale anceps (Barnard)	–	
A. pugettensis (Dana)	–	*A. bassargini* (Derzhavin)
	–	*A. punctata* (Hiwatari & Kajihara)
A. californica (Barnard)	*Apohyale bishopae* (Barnard)	*A. uragensis* (Hirayama)

stricted ranges, mostly in southern British Columbia and northern Washington state. Limitations in collecting methodology may have contributed to these narrow ranges. Subgenus *Leptohyale* is endemic to the eastern Pacific. The range of its single known species is boreal, similar to that of wider-ranging species within subgenus *Boreohyale*.

By contrast, all species of subgenus *Protohyale* are warm temperate and subtropical, ranging north to southern Japan in the west, and north from Baja California to southern California in the eastern Pacific. At least two species of the subgenus occur in Hawaii. Genus *Lelehua* occurs only in subtropical Japan in the western Pacific, but two related species are also known from Hawaii.

A similar taxonomic examination of the saltators reveals that two species of genus *Parhyale* are known from subtropical and warm-temperate waters of Japan; but none has yet been recorded from warm-temperate Baja California in the eastern Pacific. Two species are also known from the Hawaiian archipelago. Two species of genus *Ptilohyale* are known from the temperate- warm-temperate waters of the western Pacific, one from the eastern Pacific , and *Ptilohyale iole* is also known from Hawaii. Within the most intertidal and advanced genus *Apohyale*, four species occur in temperate to tropical waters of the western Pacific, only one of which (*A. bassargini*) ranges north to Hokkaido. Of the three species in the eastern Pacific, only one (*A. californica*) is warm-temperate , and the most primitive and least terrestrial species, *A. anceps*, ranges into subarctic waters of Alaska and the Aleutians.

Biogeographical counterpart taxa of the eastern, central, and western Pacific regions.

The present study indicates that, based on numbers of described species, diversity within North Pacific hyalids is highest along the North American coast (29 spp.), lower in the western North Pacific (Japan, Korea, Russia) (14 spp.), and is lowest in the central Hawaiian archipelago (9 spp.) (Table IV). Paradoxically, the diversity of hyalids at generic, subgeneric and subgroup level is highest in the western Pacific (8), and lowest along shores of the central (6) and eastern Pacific (6). Also, the number of shared genera and subgroups is equally high between western and central (6) and western and eastern regions (6), and least between central and eastern regions (4).

Thus, the modern hyalid amphipod fauna of the western North Pacific (Japan) and the Hawaiian archipelago exhibits a relatively high degree of similarity, whereas that of the Hawaiian archipelago and the eastern Pacific is relatively low. The differences may be partly attributable to greater extent of subtropical and warm-temperate marine regimes in Hawaii and the western Pacific. The latter includes southern Japan and the eastern East China Sea, and Sea of Japan (Table III, zones 1 and 2). The extent of warm-water regimes of Baja and Southern California on the Pacific coast of North America is much less (Table III, zones 9 and 10).

Although regional hyalid species inventories are not yet complete, particularly for the western Pacific (Hiwatari, pers. comm.), the present results at generic and higher group levels within family Hyalidae seem unlikely to be altered significantly by further species descriptions.

The present result for hyalid amphipods contrasts with that of Myers (1991) who compared selected corophioidean amphipod faunas of the Hawaiian archipelago with those of adjacent Pacific subregions. Corophioidean species group similarity was found highest between Hawaii and the tropical Eastern Pacific, less strong with Indo-Pacific regions, and virtually non-existent between Hawaii and the western North Pacific, including Japan.

Plausible accounting for the differing results remains speculative. Indirect evidence suggests that antiquity of the Hyalidae and other talitroidean amphipod families is markedly greater (extending well back into the Mesozoic), than that of the relatively modern superfamily Corophioidea and its family subgroups (Bousfield 1982, 2001a, 2001b; Bousfield & Shih 1994). The "hot spot" origin and geological history of the Hawaiian-Emperor island chain, connected the "proto" Hawaiian Archipelago with western Pacific continental shores initially 40+ m. y. previously (Graham 1981). Perhaps, therefore, an allopatric model of speciation might reasonably account for current taxonomic similarities, at both ends of the chain but originating at the western end, in amphipod groups that experienced similarly lengthy evolutionary histories.

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